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Research article

Evaluating the effects of wolf culling on livestock predation when considering wolf population dynamics in an individual-based model

Oksana Grente ✉[1], Sarah Bauduin[2], Nina Luisa Santostasi[3], Simon Chamaillé-Jammes[1], Christophe Duchamp[4], Nolwenn Drouet-Hoguet[5] and Olivier Gimenez[1]

[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[2]Office Français de la Biodiversité, Direction de la Recherche et Appui Scientifique, Service Conservation et Gestion des Espèces à Enjeux, Juvignac, France
[3]Sapienza University of Rome, Department of Biology and Biotechnologies, Roma, Italy
[4]Office Français de la Biodiversité, Direction de la Recherche et Appui Scientifique, Service Conservation et Gestion des Espèces à Enjeux, Gap, France
[5]Office Français de la Biodiversité, Direction de la Recherche et Appui Scientifique, Service Conservation et Gestion des Espèces à Enjeux, Gières, France

Correspondence: Oksana Grente (oksana.grente@gmail.com)

The efficiency of the management of predations on livestock by gray wolves (*Canis lupus*) through culling is under debate. Evaluating wolf culling efficiency requires to simultaneously analyze the effects of culling on the wolf population and the repercussions of these population changes on livestock predation. This protocol is technically difficult to implement in the field. To properly assess culling efficiency, we provided an integrated and flexible individual-based model that simulated interactions between wolf population dynamics, predation behavior and culling management. We considered many social processes in wolves. We calibrated the model to match the Western Alps as a case study. By considering the prey community in this area and the opportunistic nature of wolf predation, we assumed that predation on livestock at the wolf territory level increased with pack's food needs. Under this assumption and considering livestock availability as high and livestock vulnerability as uniform in space and time, culling maintained wolf population size and predation risks at low levels. Contrary to what was expected, culling decreased the mean annual proportions of dispersing wolves in our simulations, by speeding settlement. This population-level mechanism compensated for the high mortality and the pack instability caused by culling. Compensation was however dependent on the selectivity and the timing of culling. When executed before the natural mortality module in our model, the selective culling could undermine replacement of lost breeders and therefore decrease wolf population resilience to culling. Our model gives insights about culling effects in one

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specific simulated context, but we do not expect that our assumption about predation behavior necessarily holds in other ecological contexts and we therefore encourage further explorations of the model.

Keywords: *Canis lupus*, integrated model, lethal removal, livestock damages, pack duration, simulation

Introduction

Culling of large predators is the most controversial management tool used to reduce their predations on livestock, i.e. depredations (Rigg et al. 2011, Lute et al. 2018). Besides ethical reasons or risks on predator population viability, doubts about the efficiency of culling fuels public debate and controversy (Treves et al. 2019). If the most straightforward effect of culling is immediate reduction in abundance of the targeted species (e.g. for Eurasian wild boars *Sus scrofa,* Boadella et al. 2012), culling can also lead to unintended consequences, such as increased movements of surviving individuals (e.g. for badgers *Meles meles,* Prentice et al. 2019, or feral cats *Felis catus,* Lazenby et al. 2015), which may undermine culling efficiency (Elbroch and Treves 2023).

For gray wolves *Canis lupus* (hereafter, wolves), culling can disrupt the primary social units, breeding pairs, or the secondary social units, packs. Resident adults have the highest natural survival rates among wolves (Blanco and Cortés 2007, Marucco et al. 2009). If breeders die at higher rates compared to situations without culling, wolf population dynamics is likely to be accelerated with more turnovers of breeding pairs or packs (Jędrzejewski et al. 2005, Borg et al. 2015, Milleret et al. 2017). Culling is expected to reduce pack size (Brainerd et al. 2008, Ausband et al. 2017), pack duration length (Milleret et al. 2017) and reproduction rates (Cassidy et al. 2023), and to increase the movements and dispersal of wolves (Jędrzejewski et al. 2005, Brainerd et al. 2008).

There is no consensus about how these potential changes in population structure and dynamics could affect depredation levels. This is because individual and pack characteristics can influence depredation behavior in different ways. For example, studies showed that dispersing wolves were less likely (Fabbri et al. 2018), as likely (Fritts et al. 1992) or more likely (Imbert et al. 2016) than resident wolves to prey upon livestock. Several studies concluded that depredation risks increased with pack size (Treves et al. 2002, Bradley et al. 2015), whereas others found packs involved in depredations were medium-sized (Wydeven et al. 2004).

These discrepancies in depredation behavior could result from the multifactorial nature of the predation process. The diversity of wild prey that solitary wolves can kill may be reduced compared to those for wolves in packs, which may increase their attempts to predate unprotected livestock (Fritts et al. 1992, Fabbri et al. 2018). The encounter rates with livestock of dispersing wolves may also be higher due to their higher rates of movements, potentially favoring depredations by these wolves (Elbroch and Treves 2023). On the contrary, resident wolves may better know flock habits and

learn how to foil protective measures (IPRA 2020), possibly explaining why sometimes resident wolves were more likely to prey upon livestock than dispersing wolves (Fabbri et al. 2018). In addition, solitary wolves have lower food needs than breeders during summer, as they do not have pups to feed (Wydeven et al. 2004). Moreover, depredation behavior is highly context-dependent. In Yellowstone National Park (YNP) in the USA, hunting with other pack members is required to successfully take down large prey such as elk *Cervus elaphus* (MacNulty et al. 2012) or bison *Bison bison* (MacNulty et al. 2014). In southern Europe, wolves rely on smaller and more vulnerable prey, such as juvenile wild boar *S. scrofa* or roe deer *Capreolus capreolus* (Mattioli et al. 2004, 2011, Anceau et al. 2015, Imbert et al. 2016, Lagos and Bárcena 2018). Therefore, a wolf's need to hunt in a group may be reduced in this situation (IPRA 2020), as suggested by the lower mean pack size in southern Europe (e.g. 6.2 in Portugal, Nakamura et al. 2021) compared to the USA (e.g. 11 in YNP, Stahler et al. 2006).

Consequently, a proper test of the efficiency of culling in reducing depredation rates would require to simultaneously analyze 1) the effects of culling on the predator population and 2) the repercussions of these population changes on depredation levels. So far, studies focused on linking observed measures of culling and their effect on depredation but without accounting for predator population changes (Bjorge and Gunson 1985, Bradley et al. 2015, Fernández-Gil et al. 2016, DeCesare et al. 2018, Santiago-Avila et al. 2018). No consensus has emerged from these studies, with culling possibly leading to negative, positive or no effect on depredations. Their approaches lead to uncertainty about the biological mechanisms responding to culling and to high risks of bias due to confounding factors. The lack of integrated studies partly explains why there is still no clear assessment of wolf culling efficiency and why this subject remains controversial.

Only one study used simulations to model the entire process of wolf depredation management by culling (Haight et al. 2002). This study used an individual-based approach. By modelling each individual of the population, individual-based models (IBM) allow the explicit consideration of the biological mechanisms at the individual-level in order to understand the overall functioning at the population-level (Railsback and Grimm 2019). This type of modelling is particularly adapted to represent social species that exhibit complex individual interactions (Pitt et al. 2003), such as wolves. If well parameterized, simulations are good alternatives to experimental studies that are very difficult to implement like the evaluation of large predator culling effects (Elbroch and Treves 2023). Simulations are simplifications of the true processes, especially in ecology, but they can

provide insights about the general underlying mechanisms of complex systems involving many interactions (DeAngelis and Diaz 2019). However, the model of Haight et al. (2002) lacked many social processes known to occur in wolves and that can alter culling effects on population dynamics and structure, such as pack dissolution risks varying according to the number of lost breeders (Cassidy et al. 2023), replacement of missing breeders by subordinates (Caniglia et al. 2014), budding (Brainerd et al. 2008) or adoption of young wolves (Jędrzejewski et al. 2005). Moreover, they modeled depredation behavior as a binary process that was permanent once learned, which is currently not supported by literature (Berezowska-Cnota et al. 2023).

Bauduin et al. (2020) modeled wolf population dynamics through an IBM and included the social processes that were missing in Haight et al. (2002) and in other IBM of wolves (Marucco and McIntire 2010, Chapron et al. 2016). The IBM of Bauduin et al. (2020) is not spatially explicit, but the modeling of pack membership for each individual acts as a proxy for territories and therefore for the spatial dimension. Here, we extended the IBM of Bauduin et al. (2020) by modelling depredation behavior and culling. Our aim was not to provide a model for management (e.g. to determine an optimal culling quota) but to explore, in a theoretical, simple and local context, interactions between culling, population-level mechanisms and depredation when using the most complete available IBM of wolves. As a case study and similarly to Bauduin et al. (2020), we calibrated the model to simulate wolf populations from the Western Alps. In this region, depredations by wolves are common during summer in mountainous pastures and culling of wolves has been applied on the French side for approximately 15 years to reduce depredations (Ministère de l'Ecologie, de l'Energie, du Développement durable et de l'Aménagement du territoire and Ministère de l'Agriculture et de la Pêche 2008). We updated the model with the latest available data in literature. To compensate for lack of information regarding individual depredation behavior, we explored this behavior following a literature review. We tested three culling scenarios, two culling timings and explained culling effect on depredation level through its effects on wolf population structure and dynamics.

Material and methods

Modelling wolf population

We built on the IBM developed in Bauduin et al. (2020) to simulate wolf population and its dynamics. The IBM was designed as a cycle. Each cycle was designed to represent one year, starting in spring with reproduction, and consisted in a succession of 13 modules. The order of these modules and the mechanisms they simulated are detailed in Fig. 1. All individuals of the population successively moved from one module to another. Each module was triggered once during a cycle (hereafter, year). Individuals could be affected by a module or not, depending on their individual and pack characteristics. Individuals were defined as female or male, pup (1 year old), subadult (2 years old) or adult, dispersing or resident, and if resident, they could be breeder or subordinate. Packs could only have one breeding pair. Each individual and each pack had a unique number ID that could not be reattributed, even at the death of individuals or packs.

We used the model version of Bauduin et al. (2020) that assumed sex-biased breeder replacement (Fig. 1), i.e. female subordinates preferentially tended to replace missing breeders within their natal pack, whereas males usually acceded to breeding position by leaving their natal pack (Jędrzejewski et al. 2005, Vonholdt et al. 2008, Caniglia et al. 2014). We used the same parameters as in Bauduin et al. (2020) to calibrate as best as possible the model for wolf populations from the Western Alps, except the emigration parameter that we set to 33% of dispersing individuals, in order to match with the results found in the Italian Alps (Marucco et al. 2009). As there was no information about adoption frequency in this area, we used the 7 pack histories over 8 years in Poland from Jędrzejewski et al. (2005) to calculate the adoption frequency, by dividing the number of adoption events (n=2) by the number of individuals that dispersed but showed other strategies of establishment than adoption (n=14). The resulting adoption frequency of 14% was consistent with Mech and Boitani (2003) who supposed adoption frequency between 10 and 20%. No estimate was available for budding success, whether in Europe or elsewhere, therefore we used the medium value of 0.5 among those tested in Bauduin et al. (2020). Model sensitivity to adoption or budding parameters was low according to the results of Bauduin et al. (2020) because different model outputs varied by less than 20% when applying ±5% to the baseline adoption and budding parameters.

We updated the pack dissolution module from Bauduin et al. (2020) with results from Cassidy et al. (2023) in five US National Parks, in which pack dissolution risks were estimated for all pack sizes and accordingly to the status of the dead wolves in the pack. We used the best-fit generalized linear mixed model (GLMM) in Cassidy et al. (2023) to calculate the annual pack dissolution risk $p_{dissolution}$ of each pack in the pack dissolution module as:

$$p_{dissolution} = 1 - \frac{1}{1 + \exp\left(-\left(\begin{array}{l}\beta_{intercept} + \beta_{PSep} \times PS_{ep} + \\ \beta_{DWep} \times DW_{ep} + \beta_{DB} \times DB\end{array}\right)\right)} \quad (1)$$

where PS_{ep} is pack size excluding pups, DW_{ep} is the number of dead wolves excluding pups, DB is the number of dead breeders, and $\beta_{intercept}$, β_{PSep}, β_{DWep} and β_{DB} are the estimated parameters from Cassidy et al. (2023) sampled within a normal distribution of means 0.870, 0.229, −0.309 and −1.239 and of standard deviations 0.227, 0.036, 0.143 and 0.353, respectively. Therefore, the risks for pack dissolution were higher when one breeder died (e.g. $p_{dissolution} = 0.50$ for

A ♂ subordinate of 2+ years old is randomly chosen to be the new breeder if the position is vacant in his pack. The sample is among the ♂s the least related to the ♀ breeder if any. If the breeders are too related, a new ♀ breeder is sampled among the ♀ subordinates the least related to the new ♂ breeder.

A number of pups of 0-year-old is produced in every pack with a breeding pair by sampling within a Poisson distribution ($\lambda = 6.1$) [1].

All individuals age 1 year.

Each dispersing individual of 2+ years old succeeding a Bernoulli trial occupies a new territory alone.

Wolves of 16 years die [2]. Each other wolf dies if succeeding a Bernoulli trial, whose parameter is sampled within a Normal distribution that differs between pups ($\mu = 0.602$, $\sigma^2 = 0$) [3], other resident wolves ($\mu = 0.18$, $\sigma^2 = 0.04$) [4] and dispersing wolves ($\mu = 0.31$, $\sigma^2 = 0$) [5].

Each dispersing individual of 2+ years old succeeding two Bernoulli trials pairs up with a random unrelated subordinate of 2+ years old of opposite sex. They become breeders of a new pack.

If the number of packs equals the carrying capacity (*i.e.* 10), the Bernoulli parameter for resident wolves (except pups) becomes density-dependent [6].

Each dispersing ♀ of 2+ years old succeeding a Bernoulli trial pairs up with a random unrelated dispersing ♂ of 2+ years old. They become breeders of a new pack.

Each wolf disperses if its pack has at least one dead member of 2+ years old and if its pack succeeds a Bernoulli trial (Eq. 1) [7].

Dispersing individuals of 2+ years old are randomly chosen to replace missing breeders, starting with ♀s. New breeders cannot be related to any left breeder.

A ♀ subordinate of 2+ years old is randomly chosen to be the new breeder if the position is vacant in her pack. The breeding ♂, if any and related to her, loses his breeding position.

For each pack succeeding a Bernoulli trial ($\lambda = 0.14$) [9], $PS_{max} - PS$ subordinate positions are randomly attributed to 1-3 years old dispersing ♂s then ♀s. PS is recalculated, but not PS_{max}.

0, 1 or 2 new dispersing individuals of random ages and random sexes integrate the population. 1/3 of dispersing wolves are randomly chosen and emigrate [4].

The subordinates from a sample of size

$$PS_{max} - PS$$

with age-related weights [8] disperse from each pack. PS is pack size. PS_{max} is sampled for each pack within a Normal distribution ($\mu = 4.405$, $\sigma^2 = 1.251$) [2].

Wheel labels:
13 — Breeding access to ♂ subordinates / Reproduction
1 — Reproduction
Aging
2 — Culling
Natural mortality
3 — Culling
Pack dissolution
4 — Breeding access to ♀ subordinates
Dispersal
5
Migration
6
Adoption
7
Breeding access to dispersing wolves
8
9 — Pairing
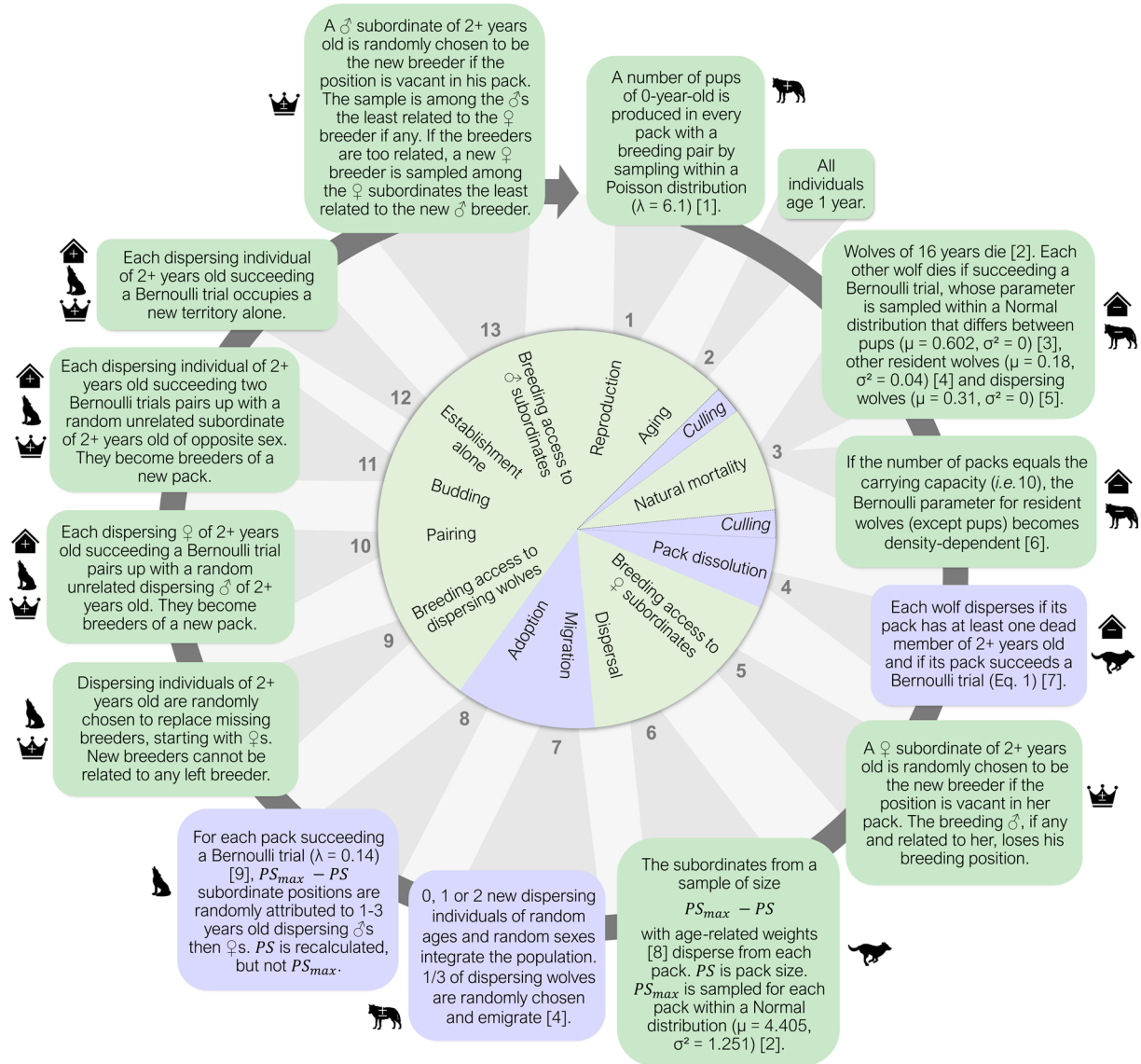10 — Budding
11 — Establishment alone
12

Figure 1. Overview of the wolf life cycle of the individual-based model (IBM), starting with the module *Reproduction* and ending with the module *Breeding access to male subordinates*. The 10 modules in green are strictly identical to the modules from the IBM of Bauduin et al. (2020). The modules in light purple are also from the IBM of Bauduin et al. (2020) but have been adapted, except the culling module which is new and described in the main text. Two timings are tested for this module: before or after the module of natural mortality. Icons indicate the modules where wolves can be added, deleted or both (standing wolf icon with +, - or ±, respectively), where the resident status can be gained (howling icon) or lost (running icon), where the breeding status (i.e. dominant) can be gained, lost or both (crown icon with +, - or ±, respectively) and when territories can become occupied or vacant (home icon with + or -, respectively). The modules are applied separately to each wolf or pack, except the sample of the Bernoulli parameter in the natural mortality module which is applied once for each class (pups, other resident wolves and dispersing wolves). Orders of adopting packs (module 8), of packs for breeder replacement (9), of establishing females (10) and of establishing individuals (11) are random. In modules 10, 11 and 12, the parameter of the Bernoulli trial is density-dependent and is equal to the difference between the carrying capacity (i.e. 10) and the number of packs, divided by the carrying capacity. In module 11, the second Bernoulli trial parameter is 0.5, as in Bauduin et al. 2020. Relatedness threshold was defined at 0.125, as in Bauduin et al. 2020. The mentioned Eq. 1 in module 4 is from the main text. *Individuals of 2+ years old* means wolves of 2 years or more, i.e. sexually mature wolves. References: 1) Sidorovich et al. 2007; 2) Marucco and McIntire 2010; 3) Smith et al. 2010; 4) Marucco et al. 2009; 5) Blanco and Cortes 2007; 6) Cubaynes et al. 2014; 7) Cassidy et al. 2023; 8) Haight and Mech 1997; 9) Jędrzejewski et al. (2005).

$PS_{ep}=3$ and estimated parameters equal to means) compared to the death of a subordinate (0.22), but were lower compared to the death of both breeders (0.82). This equation also predicts that $p_{dissolution}$ was not null but equal to 21% for pairs (of breeders or not) even when there were no deaths. Pack dissolution is yet unlikely when there is no death of wolves, especially of breeders. For example, Milleret et al. (2017) recorded no divorce (i.e. where both pair members would be observed in a new pair after a dissolution event) for 153 different wolf pairs in Scandinavia during 14 years. We therefore excluded from pack dissolution module all packs for which no adult or subadult died during the ongoing year (i.e. $DW_{ep}=0$). We also forced pack dissolution when only pups remained in a pack, as in Bauduin et al. (2020). We tested the model sensitivity to the pack dissolution module by increasing or decreasing by 5% the means of parameters $\beta_{intercept}$, β_{PSep}, β_{DWep} and β_{DB} at the same time. We considered the model to be sensitive to this set of parameters if the results varied by more than 20% (Bauduin et al. 2020).

Modelling depredation behavior

In the Western Alps, the practice of transhumance brings each summer many sheep flocks for extensive grazing. Depredations by wolves in this area mainly occur during this period (Grente et al. 2022). To mimic the Western Alps situation, we therefore modelled depredation behavior during the summer period and assumed that availability of livestock was not a limiting factor in our model.

We placed the modelled population of wolves in the context of a controlled environment, like in an experimental study. Therefore, we assumed that all wolf territories presented the same biotic and abiotic resources. Thus, we assumed that all flocks presented the same level of protection and therefore of vulnerability across all wolf territories and across years. We did not simulate any form of relative abundances between wild and domestic prey as we assumed unlimited availability of sheep.

Thus, the differences in depredation behavior simulated in our model were only due to individual or pack differences, and not to environmental or farming variables considered as equal between wolf territories and constant over time. This simulated experiment would resemble to a small-study site. This is why we restrained the carrying capacity of the model to 10 territories only. This would correspond to approximately 1000 km², i.e. a small mountain range in the Alps, as we used the estimated territory size of 104 km² from the wolf-saturated area of the central Apennines in Italy (Mancinelli et al. 2018) in our modelling of density-dependent natural mortality. A territory could be occupied by a resident solitary wolf or a pack of wolves.

Modelling depredation behavior of wolves is a challenging task, considering the discrepancies of the studies on the subject. We built our modelling based on the most commonly admitted features in wolves: their generalist and opportunistic nature (Mech and Boitani 2003, Guimarães et al. 2022). Wolves prey on a large range of species and target the most profitable ones, profitability being affected by abundance, energy gain but mostly vulnerability (Mattioli et al. 2011, Sand et al. 2016). For wolves, profitable prey are generally ungulate species, whether wild (MacNulty et al. 2014, Sand et al. 2016) or domestic (Torres et al. 2015, Petridou et al. 2019). In the French Alps, studies on wolf pack diets showed the opportunistic predation of wolves, with main prey identities shifting annually or seasonally according to prey profitability (Randon et al. 2020). Thus, in summer, domestic sheep *Ovis aries* could be the main prey consumed (Anceau et al. 2015) and could represent half of their diet (Poulle et al. 1997) or more for some packs (Flühr 2011), which reflects their high vulnerability to wolf predation. To our knowledge, no studies exist on the diet of solitary wolves in France, but two lone individuals were culled in 2019 and 2020 outside of the Alps because they were known to predate sheep or cattle.

Therefore, we assumed in our model that livestock was equally profitable to any wolf and that all wolves could target livestock as prey during summer, except pups as wolves generally do not start hunting before they become subadults (Mech and Boitani 2003). Following the hypothesis in Wydeven et al. (2004), we also assumed that large packs were associated with higher food needs than smaller packs or than solitary wolves. In a uniform environment as the one we modelled, we therefore assumed that the larger the pack, the higher the number of depredation events associated to the pack. We calculated the summer pack needs (PN) of each pack during the culling module (Fig. 1) by accounting for the lower food needs of pups in summer (Metz et al. 2011) as:

$$PN = PS_{ep} + \frac{1}{2}N_{pup} \tag{2}$$

Where N_{pup} is the number of pups in the pack. We therefore considered that all subadults and adults had the same individual food needs and that all pups had half the individual food needs of (sub)adults during the summer period (Eq. 2). Thus, packs with the same age composition in wolves had equal PN, independently of territory size fluctuations that are known to naturally occur (Brandell et al. 2020) and that were not simulated in our model. We set PN of resident solitary wolves and of dispersing wolves to 1.

Thus, under the assumptions of 1) unlimited livestock availability, 2) vulnerability of livestock to any wolf and 3) opportunistic wolf predation behavior, we considered that PN was a good proxy of the risks of depredations per social unit or pack, i.e. per territory, during summer. By attributing PN and therefore depredation risks to each wolf according to its pack composition, we avoided the explicit spatialization of the depredation process.

Modelling culling

We modelled three culling scenarios. Scenario 0 (S_0) was a null scenario where no culling was executed. Scenario 1 (S_1) mimicked random culling, comparable to unselective harvest intended to decrease wolf density (e.g. public harvest in the USA, DeCesare et al. 2018). In this scenario,

all wolves, including pups, had the same probability to be culled. Scenario 2 (S_2) mimicked selective culling, intended to target wolves attacking livestock in depredation hotspots (e.g. targeted removals in the USA, DeCesare et al. 2018 or defensive shooting in France, Meuret et al. 2020). Following our hypothesis about depredation behavior, we modelled that wolves with the highest PN were in territories with the highest risks of depredation and were therefore the most likely to be selectively culled. We excluded pups from potential targets of selective culling as wolves generally do not take part in the attacks during their first summer (Mech and Boitani 2003). To this end, we attributed a culling risk index (CR) to each wolf, excluding pups, during the culling module, based on their PN value. We set the interval of CR to [0, 1], CR equal to 0 or to 1 indicated no risk of culling or certainty of culling, respectively. We calculated CR by rescaling PN of each wolf over [0, 1] as:

$$CR = \frac{1}{PN_{max} - PN_{min}} \times \left(PN - PN_{max} \right) + 1 \qquad (3)$$

where PN_{min} and PN_{max} are the minimum and maximum values of pack needs. We set PN_{min} to 0 instead of 1 in order to set CR of resident solitary wolves or dispersing wolves to 0.17 instead of 0, so that their risk of being culled is not null. In order to harmonize the rescaling of PN across simulations, we capped all values of PN to 6 and set PN_{max} to 6, this number corresponding to one standard deviation (1.251) above the mean (4.4) of the distribution of maximum pack sizes in the model (Fig. 1).

In S_1 and S_2, culling was executed once per year. We tested two timings of the culling module within the modelled wolf life cycle: after (S_{1A} and S_{2A}) or before (S_{1B} and S_{2B}) the natural mortality module as both types of mortality may occur concurrently (Fig. 1). The culling module was only triggered when the wolf population was above 25 wolves. This number corresponded to approximately half of the expected population when carrying capacity was reached. We estimated this population size as the product of the carrying capacity (i.e. 10 packs) and the mean of the maximum pack size distribution (i.e. 4.4 individuals) but we allowed for a small portion of extra dispersing individuals, and therefore rounded the estimate to 50 individuals. This threshold was set to simulate culling managements that would be sufficiently intense to reveal the population-level mechanisms, but not too intense to prevent constant population extinctions.

To mimic the current culling of wolves applied in the French Alps (Ministère de la Transition Ecologique 2020), we set the culling threshold to 20% of the wolf population. Thus, when the culling module was executed for simulations of S_1, 20% of the wolf population was culled with a random selection of the culled individuals (i.e. regardless of their CR). For S_2, a Bernoulli trial was triggered for each subadult or adult of the population, with their probability of success equal to their CR. All wolves succeeding the Bernoulli trial were culled. Thus, the number of wolves culled by the

selective culling was adapted to the CR of the wolves of each year, and could be null if no wolves succeeded Bernoulli trials, for example because of low CR. In the case the number of wolves succeeding Bernoulli trials exceeded the culling threshold of 20% of the wolf population, a random selection corresponding to the culling threshold was done among these wolves; the selected wolves were then culled.

Model initialization

We did not initialize the IBM with a specific initial wolf population but we relied on the immigration module to simulate natural colonization, as in the French Alps (Poulle et al. 1997). To immediately start the colonization, we forced the immigration module to return two individuals during the first year. We ran each simulation of the IBM for a period of 100 years, in order to provide enough time for the simulated populations to grow. Each simulation corresponded to only one culling scenario, i.e. S_0, S_{1A}, S_{2A}, S_{1B} and S_{2B}, hence giving 5 final scenarios.

In total, we ran 250 simulations of each scenario. We used NetLogoR ver. 0.3.11 (Bauduin et al. 2019) to run the individual-based model in R ver. 4.2.3 (www.r-project.org). R scripts are available in GitLab under the GNU General Public License ver. 3.0 (https://gitlab.com/oksanagrente/IBM_wolf_culling).

Result extraction

For each simulation, the characteristics (e.g. individual ID, status of residence, pack ID, PN) of all individuals of the simulated population were extracted at the end of each year. The extracted PN was updated after the modules of natural mortality and culling. For each of the four scenarios with culling, we extracted the total number of culled wolves according to their resident and breeding status at the end of each simulation.

We then computed four demographic metrics for all five scenarios to assess the effects of culling on the predator population and the repercussions of these population changes on depredation risks. First, to evaluate the depredation risks at the population level, we computed the annual mean sum of PN of each simulation. We also used this metric to evaluate the model sensitivity to the set of parameters of the pack dissolution module. Second, we computed the annual mean number of all wolves across the simulations of each scenario. Third, to evaluate the level of pack duration and therefore of pack turnover of the population, we computed the mean number of years that packs occupied their territories over the whole simulated period of each simulation. Fourth, we computed the annual mean proportion of dispersing wolves of each simulation. We explored the outliers of the distributions relative to depredation risks, pack duration and dispersal by separately computing the second metric (i.e. annual mean number of wolves) of simulations that did and those that did not produce outliers for these distributions. We defined a value as an outlier when the value was below $Q_1 - 1.5 \times (Q_3$

$- Q_1)$ or above $Q_3 + 1.5 \times (Q_3 - Q_1)$, where Q_1 and Q_3 were the first and third quantiles of the distribution.

Results

Counts and types of culled wolves

When culling was executed after the natural mortality module, the median of total count of culled wolves at the end of the simulations was higher for the random culling (S_{1A}) than in the case of the selective culling (S_{2A}) scenario, but their distributions greatly overlapped (Fig. 2a, right panel). However, this overlap was weak when culling was executed before the natural mortality module, essentially because the distribution of total count of culled wolves after 100 simulated years for S_{2B} was very narrow around its median at 63, whereas the distribution for S_{1B} was largely spread around its median at 191 (Fig. 2b, right panel).

At the end of the simulations, the culling of S_{1A} mainly removed resident wolves (99% $\pm$ 1% [mean $\pm$ SD]) and on average 30% ($\pm$ 4%) of breeders among the resident culled wolves (Fig. 2a), but in the case of S_{1B}, both distribution means were lower (96% $\pm$ 2%, 22.5% $\pm$ 3%, Fig. 2b). The annual average proportion of dispersing individuals and of pups was indeed higher before than after natural mortality because their natural survival rates were the lowest of all wolves (Fig. 1). Therefore, in the case of random culling, the execution of culling before natural mortality (S_{1B}) diluted the annual culling risks for resident and breeders. Thus, reproduction of the next cycle was less impacted in S_{1B} than in S_{1A}, hence leading to a greater increase of population size in the next cycle and eventually to a higher annual number of removals, set to 20% of the population.

At the end of the simulations, the culling of S_2 targeted much more residents and breeders than S_1 for both timings of culling. Thus, the culling of S_{2A} almost exclusively removed resident wolves (99.9% $\pm$ 0.005%) and approximately one breeder over two culled residents (47% $\pm$ 5%, Fig. 2a). The culling of S_{2B} removed only slightly less residents than S_{2A} (99.2% $\pm$ 0.01%, Fig. 2b), contrary to S_{1B} in relation to S_{1A}. This was because in S_2, dispersing wolves had the lowest annual non-zero culling risks. Therefore, the higher annual proportion of dispersing wolves facing culling in S_{2B} compared to S_{2A} could not alleviate the annual culling risks of residents as much as in S_{1B}. Meanwhile, the higher annual proportion of pups during the culling module in S_{2B} compared to S_{2A} increased the annual culling risks of resident wolves in S_{2B} by increasing their PN. Thus, these two opposite effects led to very similar total proportions of culled residents for both culling timings of S_2. In addition, the higher annual proportions of pups during the culling module in S_{2B} caused the increase of the total proportion of culled breeders (56% $\pm$ 6%) compared to S_{2A}, still by increasing their PN. Thus, contrary to S_1, reproduction was more impacted in S_{2B} than in S_{2A}. This led to smaller increases of pack sizes and population sizes, to lower pack needs and eventually to lower numbers of removals in S_{2B} than in S_{2A}.

Effect on depredation risks

Both scenarios of random culling S_1 and selective culling S_2 were efficient to reduce depredation risks, regardless of culling timing. For the null scenario S_0, the depredation risks ranged from 80.3 to 221.4 without the outliers (Fig. 3a). Compared to S_0, ranges without outliers were narrower and lower for the random culling scenario S_1 and the selective culling scenario S_2, whether the culling module was executed after (S_{1A}: [31.4–76.0]; S_{2A}: [30.9–70.4], Fig. 3a) or before natural mortality (S_{1B}: [17.3–47.5]; S_{2B}: [10.4–32.8], Fig. 4a). Distributions of depredation risks for S_1 and S_2 only overlapped with the outliers from the lower tail of the distribution for S_0, regardless of culling timing.

In addition, culling was more efficient to decrease depredation risks when it was executed before natural mortality rather than after, especially when the applied culling was selective. The medians of depredation risks were indeed reduced by 4.6 times in S_{1B} and by 6.9 times in S_{2B} compared to S_0 (Fig. 4a), whereas they were only reduced by 2.5 times in S_{1A} and by 2.8 times in S_{2A} compared to S_0 (Fig. 3a).

The depredation risks of all scenarios were not sensitive to variations in the set of parameters of the pack dissolution module (Table 1).

Effect on population size

Both scenarios of random culling S_1 and selective culling S_2 produced on average smaller wolf populations than the null scenario S_0, regardless of culling timing. For the null scenario S_0, population growth slowed approximately from year 50, and reached a mean of 44.1 individuals (95% Prediction Interval PI: [42.9–45.3]) at year 100 (Fig. 3b), which was slightly below the expected population size at equilibrium.

When the random culling and the selective culling were executed after the natural mortality module (scenarios S_{1A} and S_{2A}), population growth slowed approximately from year 25 and stabilized thereafter, reaching respectively means of 17.9 (S_{1A}, 95% PI: [17.3–18.5]) and 17.2 (S_{2A}, 95% PI: [16.6–17.8]) at year 100, which was 2.5 and 2.6 times lower than the mean for S_0 (Fig. 3b).

When the random culling and the selective culling were executed before the natural mortality module (scenarios S_{1B} and S_{2B}), population growth slowed much earlier than in S_{1A} and S_{2A}, approximately from year 10 (Fig. 4b). Culling could indeed start earlier in S_{1B} and S_{2B} (medians: 17 years) than in S_{1A} and S_{2A} (medians: 26 and 28 years) because the population could more rapidly reach the threshold of 25 individuals in the culling module when the natural mortality module occurred afterwards. Population sizes in S_{1B} and S_{2B} also stabilized, reaching respectively means of 10.3 (S_{1B}, 95% PI: [9.8–10.8]) and 7.4 (S_{2B}, 95% PI: [6.9–7.8]) at year 100, which was 4.3 and 6.0 times lower than the mean for S_0 and 1.7 and 2.3 times lower than the means for S_{1A} and S_{2A}, respectively.
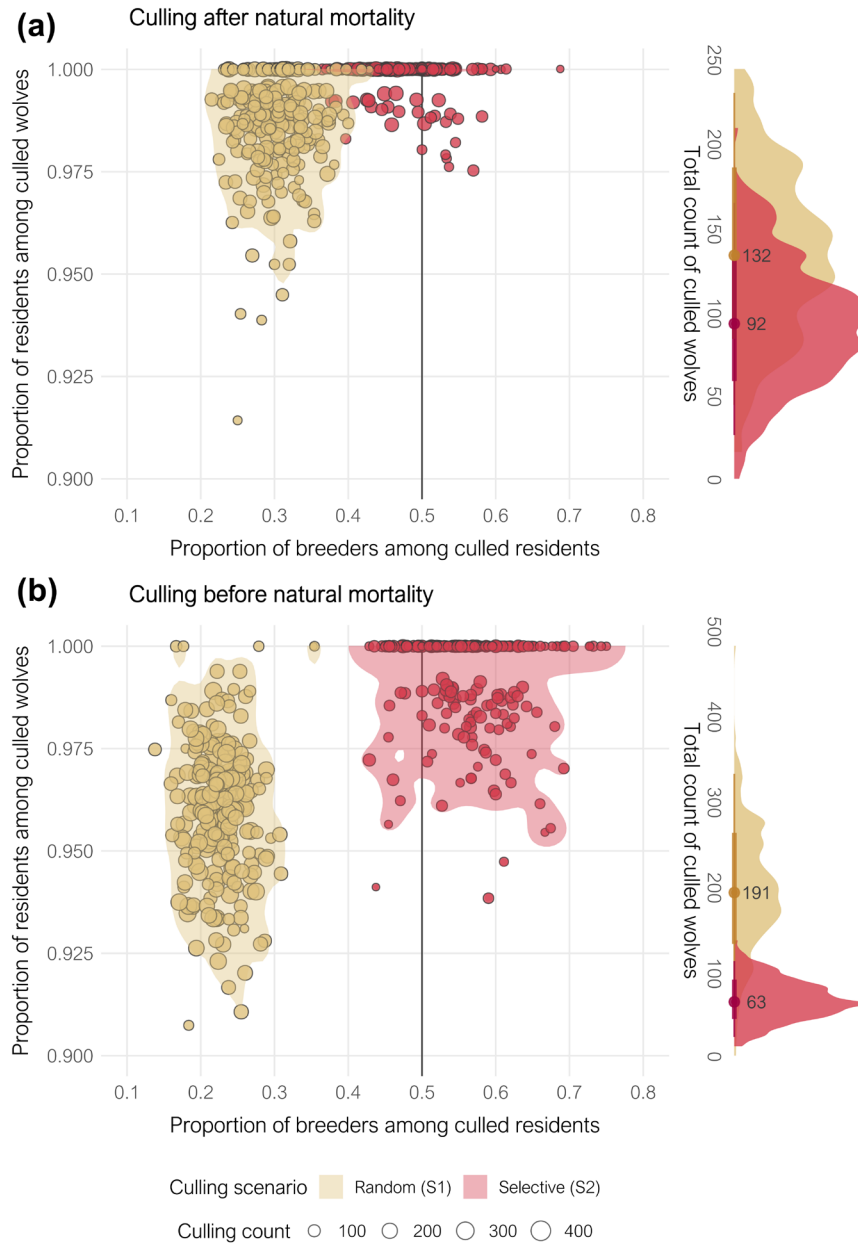
Figure 2. Types and counts of culled wolves for the random culling S_1 (yellow) and the selective culling S_2 (red) scenarios, with culling executed after (S_{1A} and S_{2A} in panel a) or before (S_{1B} and S_{2B} in panel b) the natural mortality module. Each point represents the output of one of the 250 simulations of each culling scenario, at the end of the simulated period of 100 years. The x-axis and y-axis are the proportions of breeders and of residents among all culled residents and all culled wolves, respectively. Size of points represents the total number of culled wolves in the simulation. Filled contours represent 95% of the highest density region of each dataset, except the dataset of S_{2A} (a) that could not be computed due to its very skewed distribution. The distributions of the total number of culled wolves per simulation at the end of the period of 100 years are given on the right of the panels; the intervals at the bottom of the distributions show the 66% (thick line) and 95% (thin line) prediction intervals along with the annotated medians (point).

Effect on pack duration

Both scenarios of random culling S_1 and selective culling S_2 generally produced more pack turnover than the null scenario S_0, regardless of culling timing. For the null scenario S_0, the pack duration ranged from 4.3 to 26 years, with a median at 15.9 years (Fig. 3c). Compared to S_0, ranges were narrower and lower for the random culling scenario S_1 and for the selective culling scenario S_2, whether the culling module was executed after (S_{1A}: [5.3–12.7]; S_{2A}: [5.5–12.5], Fig. 3c) or before natural mortality (S_{1B}: [3.8–12.1]; S_{2B}: [3.3–9.2], Fig. 4c). Distributions for S_1 and S_2 for both culling timings only overlapped with the lower 25% of the distribution for S_0.
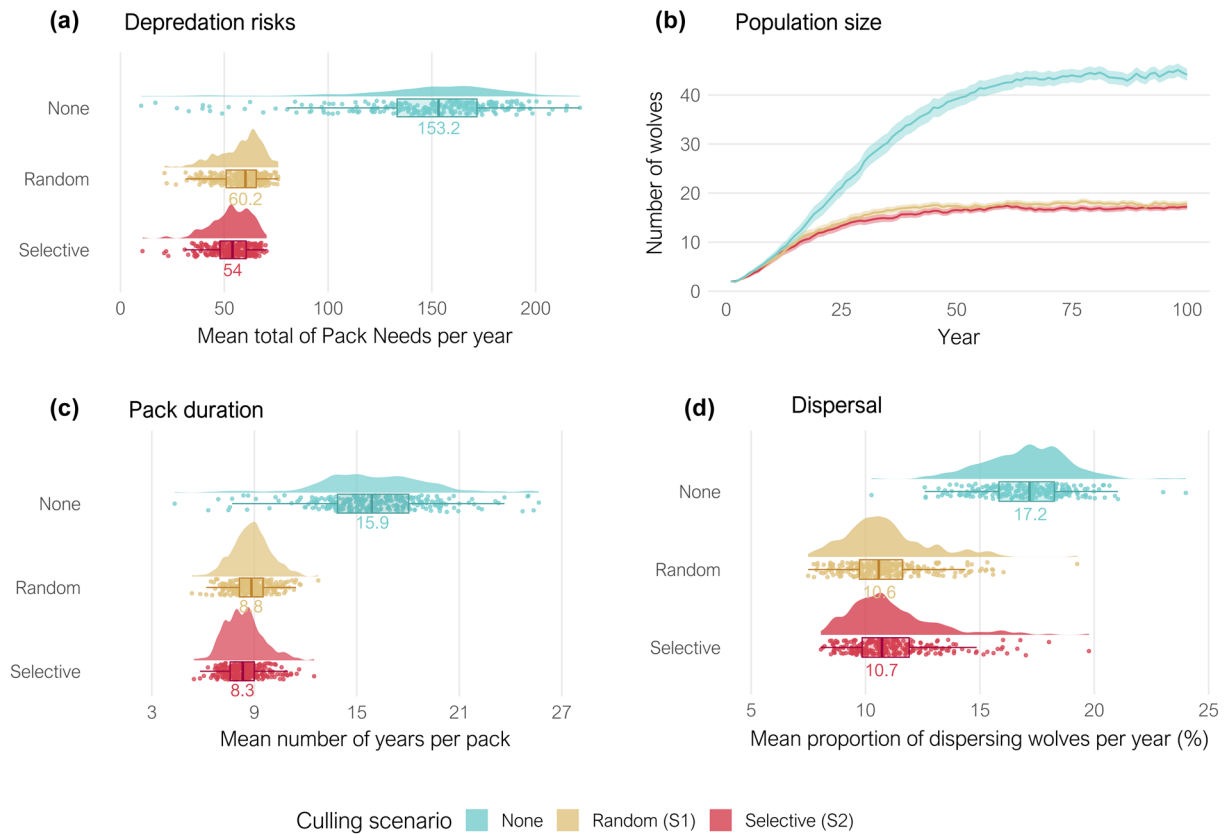
Culling after natural mortality

Figure 3. Results of the four demographic metrics computed for the 250 simulations for each of the three culling scenarios, no culling S_0 (blue), random culling S_{1A} (yellow) and selective culling S_{2A} (red), with culling executed after the natural mortality module. Each point in panels a, c and d is the result of one simulation. Each annotated value below boxplots in panels a, c and d is the median of the distribution. Each point in panel a is the total sum of pack needs (PN) of all wolves updated after the modules of natural mortality and culling of each year, averaged across all years for each simulation. Panel b displays the number of wolves at the end of each year, averaged across all simulations of each culling scenario, and the 95% prediction interval of the mean. Each point in panel c is the number of years that packs (i.e. at least two individuals within the same territory) occupied their territories during the whole simulation, averaged across all packs for each simulation. Each point in panel d is the percentage of dispersing wolves in the population at the end of each year, averaged across all years for each simulation.

In addition, pack duration was generally lower when culling was executed before natural mortality rather than after, especially when the applied culling was selective. The medians of pack duration for S_{1B} and S_{2B} were indeed respectively 14% and 31% lower than those for S_{1A} and S_{2A}. If both S_{1A} and S_{2A} produced comparable distributions of pack duration (Fig. 3c), S_{2B} produced a narrower distribution than S_{1B}, with its median being 25% lower than in S_{1B} (Fig. 4c).

Effect on dispersal

Contrary to our expectations, both scenarios involving culling (S_1 and S_2) generally produced lower proportions of dispersing wolves within the population than the scenario without culling (S_0), regardless of culling timing. The medians of the random culling scenarios S_{1A} (10.6%) and S_{1B} (9.9%), and of the selective culling scenarios S_{2A} (10.7%) and S_{2B} (12.5%) were all lower than the median of S_0 at 17.2% (Fig. 3d, 4d).

Excluding outliers, only the upper 25% of distributions for S_{1A}, S_{2A} and S_{1B} overlapped the lower 25% of the distribution for S_0. In the case of S_{2B}, the overlap with the null distribution was more pronounced, and corresponded to roughly 50% of both distributions (Fig. 4d).

In addition, the median of the proportion of dispersing individuals was lower when the random culling was executed before natural mortality rather than after, but it was the opposite for the selective culling. S_{2B} generally produced higher proportions of dispersing individuals than the other scenarios with culling (Fig. 3d, 4d).

Outliers

The number of simulations producing an outlier value within at least one of the distributions relative to depredation risks (Fig. 3a, 4a), pack duration (Fig. 3c, 4c) and dispersal (Fig. 3d, 4d) ranged between 11 and 26 over the 250 simulations of
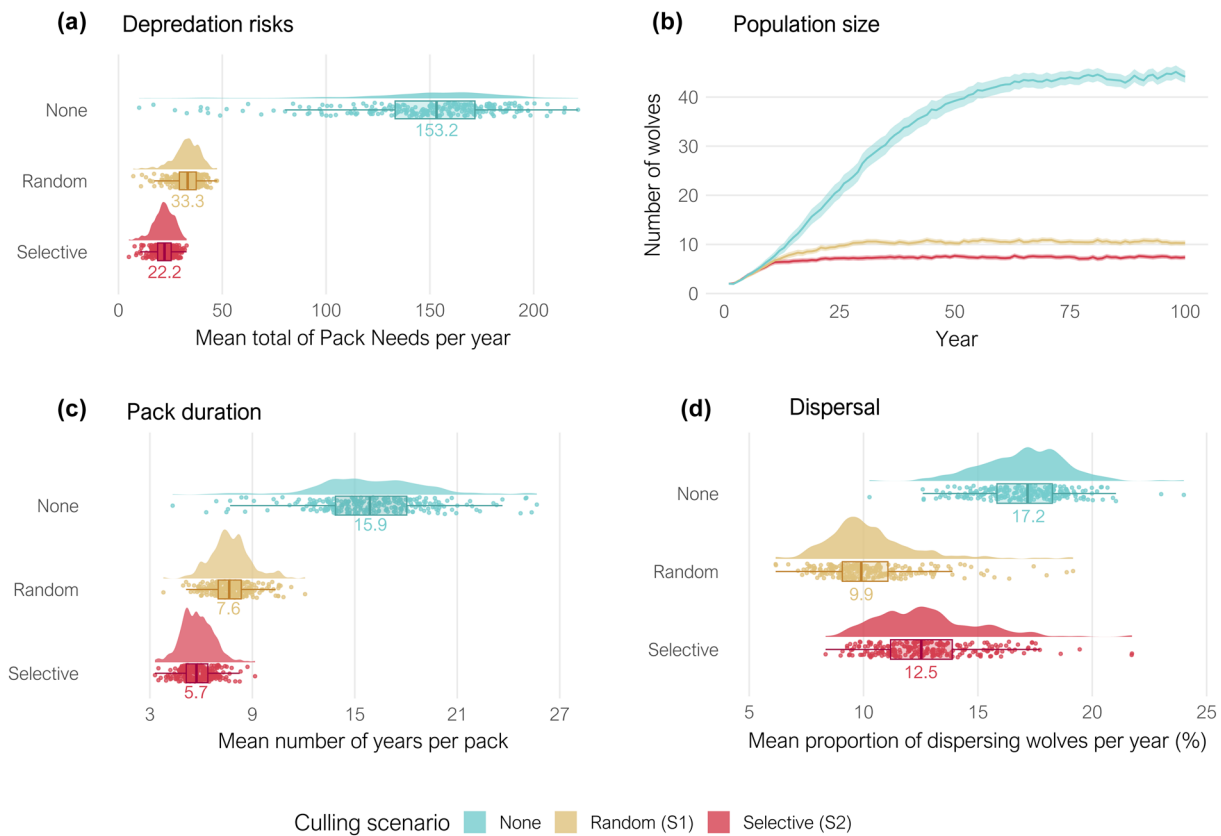
Culling before natural mortality

Figure 4. Results of the 250 simulations for each of the three culling scenarios, no culling S_0 (blue), random culling S_{1B} (yellow) and selective culling S_{2B} (red), with culling executed before the natural mortality module. Each panel was prepared as in Fig. 3.

each scenario (Fig. 5). For all scenarios, these simulations (hereafter, 'extreme') produced on average smaller population sizes than the other simulations (hereafter, 'regular'). In the null scenario, the extreme simulations were generally due to low colonization speeds, with simulated populations below those of the regular simulations by approximately 10 individuals at year 100 (Fig. 5a). When the culling module was executed after the natural mortality module, the extreme simulations were also due to low colonization speeds, but the low mean population size of the regular simulations made it easier for the populations of the extreme simulations to catch up by the end of the simulations (Fig. 5b, 5c). To a slightly lesser extent, the same assessment could be made for S_{1B} (Fig. 5d). However, for S_{2B}, the colonization speed did not seem to be blamed because the differences between both extreme and regular means of population size were

Table 1. Results of the sensitivity analysis of the model to variations in the set of pack dissolution parameters. Depredation risks (i.e. mean total of pack needs per year) were averaged across all 250 simulations for each combination of culling scenario and culling timing, and A) decreased by 20% when using the respective distribution means of 0.870, 0.229, –0.309 and –1.239 for $\beta_{intercept}$, β_{PSep}, β_{DWep} and β_{DB} of Eq. (1) in the pack dissolution module, B) obtained when increasing by 5% the distribution means of the β parameters from A, C) obtained when decreasing by 5% the distribution means of the β parameters from A, and D) increased by 20% when using the distribution means from A. We considered the model to be robust to the set of parameters of the pack dissolution module if, for each row, the mean depredation risks from columns B and C were within the range of the values from columns A and D.

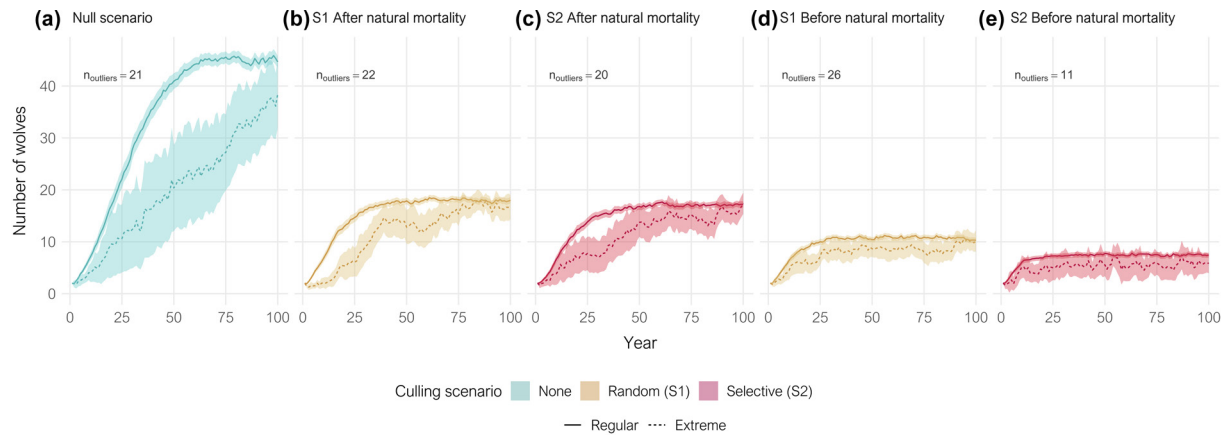| Culling scenario	Culling timing in relation to the natural mortality module	A. –20% of mean depredation risks for baseline dissolution parameters	B. Mean depredation risks for dissolution parameters at +5%	C. Mean depredation risks for dissolution parameters at –5%	D. +20% of mean depredation risks for baseline dissolution parameters
Null		118.13	149.64	150.31	177.2
Random	After	46.26	57.16	58.06	69.39
Selective	After	42.66	53.78	54.25	63.99
Random	Before	26.17	32.18	32.76	39.25
Selective	Before	17.54	20.98	21.88	26.32

Figure 5. Number of wolves at the end of each year, averaged across regular (solid line) or extreme (dotted line) simulations, and their 95% prediction intervals, for each combination of culling scenario and culling timing: (a) no-culling S_0 (blue), (b) random culling S_{1A} (yellow) and (c) selective culling S_{2A} (red) after the natural mortality module, (d) random culling S_{1B} (yellow) and (e) selective culling S_{2B} (red) before the natural mortality module. Extreme simulations corresponded to the simulations producing an outlier value within at least one of the distributions related to depredation risks, pack duration and dispersal from panels (a), (c) and (d) of Fig. 3 and 4. Their number $n_{outliers}$ is annotated on the top left of each panel. Regular simulations corresponded to all the other simulations, i.e. 250-$n_{outliers}$.

approximately constant over time, with both prediction intervals overlapping frequently from the first simulated years (Fig. 5e). The 11 populations of the corresponding extreme simulations could in fact go extinct one or several times. The selective culling could indeed remove a large proportion of breeders in a single year when executed before natural mortality, causing the population to plummet despite the settlement of several packs.

Discussion

We provided an integrated model that simulated interactions between wolf population dynamics, wolf depredation behavior and culling management. We therefore reproduced the whole process of depredation management by culling, as an exercise of simulation intended to evaluate the efficiency of culling to reduce depredations by wolves. We considered many social processes in wolf populations that could interfere with culling management and that we updated with the latest available data in literature. We intended these results to provide insights into culling efficiency in a simple, theoretical and local context, through the consideration of the culling effects on wolf population structure and dynamics.

Effects of culling on population structure and dynamics

The main effect of all simulated scenarios with culling was the reduction in wolf population size, that was on average between 2.5 and 6 times smaller than what was observed without culling. This reduction was stronger when we executed culling before natural mortality, because the wolf populations were larger and reached more easily 25 individuals when they entered the culling module in this configuration, which in turn could trigger culling more frequently with many removals.

Even though the selective culling generally removed less individuals than the random culling, reduction of population size was equal or even greater in the former scenario than in the latter. The selective culling had indeed more risks than the random culling to kill wolves in large packs, i.e. probably with a complete breeding pair, and therefore to imperil reproduction within these packs by potentially targeting breeders. On the contrary, the random culling targeted lone resident wolves, dispersing individuals or even pups, i.e. individuals which did not contribute to reproduction. This difference between culling scenarios was exacerbated when the culling module was executed before natural mortality because the higher proportions of pups during culling in this configuration caused both the increase and the reduction of the culling risks of breeders in the selective culling scenario and in the random culling scenario, respectively.

In addition, all scenarios with culling expectedly increased rates of pack turnovers and therefore pack instability of the simulated populations, by approximately reducing by half or more the average pack duration compared to the null scenario. The pack duration mean of our 1000 simulated culled populations had a higher and larger range (3.3–12.7 years) than the one observed in five US national parks (2.2–6.4 years, Cassidy et al. 2023). Besides the parameterization choices of our model (e.g. carrying capacity, southern European demographic parameters), the differences between the observed and simulated ranges could also result from the possible higher anthropogenic mortality (range: 22–58% for collared wolves, mostly culled, versus 20% simulated culling threshold), the shorter duration of the study period (range: 22–34 observed years, versus 100 simulated years), the smaller number of monitored packs (182 observed packs, versus 16 387 simulated packs) and the risk of imperfect detection in the case of the observed data.

Yet, despite increased levels of pack turnover, culled populations in our model remained on average stable.

The population-level mechanism compensating for pack instability due to culling was the reduction of the proportion of dispersing wolves by 1.4–1.7 times compared to the null scenario. This result is unexpected because culling is generally considered as increasing movements of surviving individuals, and therefore as increasing dispersal process (Jędrzejewski et al. 2005, Brainerd et al. 2008). By killing wolves in packs, sometimes leading to pack dissolution, culling sped up the settlements of dispersing wolves in our simulated area through the modules of adoption, replacement by dispersing individuals or establishment, resulting in higher resident proportions. Moreover, the loss of wolves caused by culling also decreased risks of dispersal of surviving subordinates, first by decreasing pack size in the dispersal module and second by allowing an easier access to a breeding position in the two replacement modules. Therefore, the easier settlement of dispersing individuals and the decreased risks of dispersal of subordinates both compensated for the consequences of breeder loss.

Consistently with our findings, Borg et al. (2015) also observed that harvest in Alaska increased the probability of pack dissolution but that population growth rates remained unaffected. In addition, Zubiria Perez et al. (2024) estimated stable pack persistence despite a period of harvest in Wisconsin. Both studies suggested that fast replacement by subordinates or dispersing wolves could be the compensatory mechanism to breeder loss caused by harvest, which is therefore confirmed by our simulations. Nevertheless, Borg et al. (2015) and Brainerd et al. (2008) suggested that this mechanism should be less compensatory in unsaturated and recolonizing populations, whereas our simulations showed that the mechanism still greatly compensated breeder loss and pack dissolution in populations largely below the carrying capacity.

Compensation to breeder removals could, however, be less effective for other culling strategies, for example when entire packs are extirpated (Bradley et al. 2015) or when harvest occurs before or during the breeding season (Borg et al. 2015, Zubiria Perez et al. 2024). In our case, we observed that the selective culling executed before the natural mortality module (S_{2B}) led on average to very small wolf populations and to the highest proportions of dispersing individuals across the scenarios with culling, even though this scenario removed the least individuals. This combination of culling scenario and timing greatly increased the proportion of culled breeders, which jeopardized more frequently reproduction and settlement of dispersing individuals as breeders, causing the simulated populations to be more subject to extinctions. Therefore, the undermined compensation to breeder removals in certain configurations of culling may then impact wolf population resilience and viability.

Repercussions of changes of population structure and dynamics on depredation risks

We observed that all scenarios with culling were more efficient in reducing depredation risks of simulated wolf populations than the scenario without culling. This mechanism was generated by maintaining simulated populations at low or very low levels of abundance which reduced food needs of packs.

In our model, culling efficiency to reduce depredation risks strongly depended on our assumption about depredation behavior modelling. We assumed that predation on livestock increased with pack's food needs, to match a situation that could occur within the Western Alps, according to available information and scientific literature about wolf predation behavior (Poulle et al. 1997, Wydeven et al. 2004, Mattioli et al. 2011, Anceau et al. 2015, Bradley et al. 2015, Sand et al. 2016, Petridou et al. 2019, Guimarães et al. 2022). However, the mechanisms of depredation behavior remain highly debated within the scientific community, and other modelling choices could have been made.

For example, Haight et al. (2002) modelled depredation behavior as a transmission between breeders and subadults, that was suggested in Fabbri et al. (2018) and van Liere et al. (2021), but they also modelled this behavior as permanent once learned, which is not yet supported in the literature (Berezowska-Cnota et al. 2023). Another assumption, strictly opposite to ours, supports that decreasing size of packs increases depredation risks (Treves et al. 2019, Šuba et al. 2023). This assumption suggests that large wild prey like red deer *C. elaphus* would be more profitable than small-sized livestock like sheep *O. aries* in the case where wolf pack sizes are large enough to allow adequate hunting success probabilities of large prey. Nevertheless, unprotected and abundant small-sized livestock like sheep should probably remain highly profitable to any wolf, because its vulnerability should largely compensate for its reduced energy gain compared to large prey (Mattioli et al. 2011, Sand et al. 2016). Moreover, in the Western Alps, differences in size and therefore in energy gain are small between wolf-predated wild ungulates (e.g. Alpine chamois *Rupicapra rupicapra* or roe deer *C. capreolus*) and sheep. This context should increase sheep profitability for wolves. In addition, the development of flock protection in France, especially of livestock guarding dogs (Landry et al. 2020, Meuret et al. 2020), should decrease sheep vulnerability and consequently should decrease depredation success of wolves with small or inexistent group hunting possibilities (MacNulty et al. 2012). To mimic this phenomenon, we could have modelled decreasing vulnerability of livestock over time by progressively reducing depredation risks and therefore culling risks of all wolves. The decrease of depredation risks would have been more pronounced for wolves living alone or in packs of small sizes, because their limited group hunting abilities would have prevented them from accessing to well protected livestock. However, this modelling would only have reinforced the mechanisms we already observed (e.g. efficiency of culling, breeder loss compensations, risks on wolf population viability) but would have introduced more arbitrary parameters. Therefore, we kept the depredation behavior constant over time.

Our assumption about wolf depredation behavior as a function of pack food needs could however not hold, for example if the Alpine prey community tends to change, or

in a totally different ecosystem, such as in parts of North America, where group hunting strategies by wolves may vary due to differences in prey community, agricultural practices or other environmental features. Besides the assumption about wolf depredation behavior, the modelling of the wolf life cycle and of the culling process would also need to be adapted to represent another context, with new parameters and module adjustments.

Comparison between simulation results and the French Alps situation

Despite the increase in the proportion of culled wolves in 2019 (Ministère de la Transition Ecologique et Solidaire 2020), the recolonizing wolf population in France has still not reached a steady threshold. New packs continue to settle in the French Alps (Préfecture Auvergne-Rhône-Alpes 2022), but population growth starts to show a slowdown (Préfecture Auvergne-Rhône-Alpes 2024). Assuming that our modelling of wolf depredation behavior and of culling is close to the situation in the French Alps, our simulation results could suggest that wolf culling can be partly compensated through faster settlement of dispersing wolves, but that the wolf population dynamics is slowed down by culling and that the population size will soon reach a threshold like in our simulations. Moreover, our results are consistent with preliminary analyses of the observed data of the French wolf population (Duchamp et al. 2023), which showed an increased probability for dispersing individuals to become resident after the intensification of culling.

The current culling strategy in France being selective, it remains to be seen whether it is closer to the scenario where selective culling is implemented before or after natural mortality. Because flocks are mainly grazing at high altitudes from summer onwards, most wolves in France are currently culled during summer and early fall, therefore after reproduction, after the early mortality of pups but before the mortality of dispersing individuals occurring during the fall and winter dispersal phases. Therefore, the culling applied in France may be an in-between selective culling scenario due to the concurrent nature of both natural and anthropogenic mortalities.

Meanwhile, reported attacks on livestock seem to stabilize in France from 2017, with only small variations since then (DREAL Auvergne-Rhône-Alpes 2024). Alone, these records cannot demonstrate that culling enabled this stabilization, as correlation between levels of culling and of attacks cannot infer causality (Treves et al. 2019). On the contrary, still assuming our model as valid, our simulations results could suggest that the applied culling in the French Alps should have helped to reduce predation on livestock compared to a hypothetical situation where culling would not have been applied at all.

However, our model, as a simplification of reality, implies many limits. For instance, we did not account for illegal killing, which had been shown to greatly modify the mortality rates of adults in Finland (Suutarinen and Kojola 2018). Short pack duration might also affect fitness, with reproduction of new breeding pairs possibly being less successful than the one of long-lasting pairs (Milleret et al. 2017), a potential effect that we did not model. Fitness can also be affected by inbreeding, especially in small wolf populations (Gómez-Sánchez et al. 2018) as the one we modelled. Here, we considered that the process of inbreeding avoidance known to occur in wolves (Vonholdt et al. 2008), already modelled in the initial version of the model (Bauduin et al. 2020), and the migration rates of the modelled population should have limited the occurrence of inbreeding and its negative effects on fitness. However, for wolf populations that are both small and isolated like in Scandinavia (Åkesson et al. 2022), linking fitness (e.g. reproductive success) with inbreeding level in the model would be relevant (Liberg et al. 2005) and might modulate the effects of culling on wolf population dynamics. Finally, the use by default of parameters estimated for wolf populations from North America, such as the parameters from the pack dissolution module, may not be the most appropriate ones for our simulations of the wolf population from the Western Alps. Nevertheless, the sensitivity analysis showed a limited effect of the variations of these parameters on the model.

Besides these limits related to the modelling of the wolf population, the largest limit of our model was the assumption of an experimental homogeneous environment where depredation behavior did not depend on farming or environmental variability. This condition cannot be not true at the scale of the whole French Alps. Some areas within this region may temporarily present farming or environmental features that favor predation, such as transient bad weather conditions or bushy environment that locally reduce guarding efficiency. Added to wolf density, these features should explain the predation hotspots that we observe in this region (Grente et al. 2022). Nevertheless, properly simulating all the environmental or farming variability of the Alps seems hardly reachable in a model. This also explains why our model was not conceived as a management tool for the French authorities, but as simulations of culling effects in one simple context that could arise in some localities of the French Alps, and whose results may contribute, with others, towards reaching a consensus on the controversial subject of wolf culling efficiency.

Conclusions and perspectives

Our model allowed us to properly evaluate the efficiency of culling in reducing depredation risks by wolves through the effects on the wolf population, thanks to an exercise of simulation. The modelled wolf population evolved through a detailed life cycle and in a theoretical context of uniform livestock availability and vulnerability, as it could arise in a small-scale study site. Using the context of the Western Alps as a case study, we modelled wolf depredation behavior by assuming that predation on livestock increased with food needs at the wolf territory level, following a thorough examination of literature.

Under these assumptions, culling reduced wolf population size and was efficient to reduce depredation risks. Contrary

to what was expected, culling decreased the mean annual proportions of dispersing wolves in our model, by increasing settlement speed. This population-level mechanism compensated for high rates of mortality due to culling. Compensation was however dependent on the selectivity and timing of culling regarding natural mortality. When executed before the natural mortality module in our model, culling targeting in priority packs with high food needs could undermine compensation to breeder removals and impact wolf population resilience to culling.

Despite the inevitable simplifications associated to any modelling exercise, we believe our study illustrates how individual-based modelling can contribute to lift the uncertainty about the biological mechanisms responding to culling and can help to reach a consensus on this controversial subject. Because the depredation behavior of wolves remains poorly known at the individual-level, the model may benefit from future findings. To pursue the understanding of culling effects, we therefore encourage further explorations of the model, by modelling different contexts of predation or by updating model parameters or processes with results from field-based studies, to embrace the variability inherent to the predation of livestock by wolves across the world.

Author contributions

Oksana Grente: Conceptualization (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Visualization (lead), Writing – original draft (lead), Writing – review and editing (equal). **Sarah Bauduin**: Conceptualization (supporting), Formal analysis (supporting), Investigation (supporting), Methodology (equal), Software (lead), Writing – review and editing (equal). **Nina Luisa Santostasi**: Conceptualization (supporting), Writing – review and editing (equal). **Simon Chamaillé-Jammes**: Conceptualization (supporting), Writing – review and editing (equal). **Christophe Duchamp**: Conceptualization (supporting), Writing – review and editing (equal). **Nolwenn Drouet-Hoguet**: Conceptualization (supporting), Funding acquisition (equal), Project administration (equal), Resources (equal), Supervision (equal), Writing – review and editing (equal). **Olivier Gimenez**: Conceptualization (supporting), Funding acquisition (equal), Project administration (equal), Resources (equal), Supervision (equal), Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data and scripts are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v15dv4243 (Grente et al. 2024).

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