From individual behavior and pack dynamics to population responses: An individual-based approach to model the wolf social life cycle

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Highlights

- We developed an individual-based model (IBM) simulating wolf population dynamics.
- The IBM incorporates up-to-date knowledge of pack structure and dynamics.

- The IBM is flexible and modular and can be adapted to any wolf populations.
- The IBM is written in R language to make its use by ecologists easy.

Abstract

The presence of wolf populations in human-dominated landscapes is challenging worldwide because of conflicts with human activities. Modeling is an important tool to predict wolf dynamics and expansion and help in decision making concerning management and conservation. Here we present an individual-based model (IBM) to project wolf population dynamics. IBMs are bottom-up models that simulate the fate of individuals interacting with each other, with population-level properties emerging from the individual-level simulations. IBMs are particularly adapted to represent social species such as the wolf that exhibits complex individual interactions. Our IBM predicts wolf demography including fine-scale individual behavior and pack dynamics processes based on up-to-date scientific literature. The model extends previous attempts to represent wolf population dynamics, as we included important biological processes that were not previously considered such as pack dissolution, asymmetric male and female breeder replacement by dispersers or subordinates, inbreeding avoidance, establishment of dispersing individuals by budding, adoption of young dispersing wolves, long distance dispersal, and density-dependent mortality. We demonstrate two important aspects of our IBM (i.e., modularity and flexibility) by running different series of the processes representing the wolf life cycle. The simulations point out the importance of data records on these biological components when managers are willing to promote wolf population conservation and management strategies. This exercise also shows that the model can flexibly include or exclude different processes therefore being applicable to wolf populations experiencing different ecological and demographic conditions. The model is coded in R to facilitate its understanding, appropriation and adaptation by ecologists. Overall, our model

allows testing different scenarios of wolf dynamics, disturbances and alternative management strategies to project wolf populations, and therefore inform decision making to improve wolf management and conservation.

Key words

Gray wolf, Individual-based model, Pack dynamics, Population projection, R language, Wildlife management

Abbreviations

IBMs: individual-based models

ID: identity

Fig.: Figure

ODD: Overview, Design concepts, and Details

popDensStd: wolf density per 1000 km2 standardized with Cubaynes' mean and standard deviation

sd: standard deviation

1. Introduction

Gray wolf (*Canis lupus*) has been extirpated from most of the globe during the last century due to its competition with humans for wild preys, depredations on livestock and general persecution (Ripple et al., 2014). Then, most of the remaining populations were considered endangered in the early 20th (Mech and Boitani, 2003). However, numerous wolf populations are now under protection regimes and management actions favor species persistence or comeback (Chapron et al., 2014). Even though the presence of this large carnivore may play an important role in maintaining a healthy ecosystem and increase biodiversity, its recolonization is challenging. For examples, the impact wolves exert on human activities such as livestock farming (Kaczensky, 1999; Lute et al., 2018), or the increasing threat of hybridization with dogs in human-dominated landscapes (Pilot et al., 2018; Randi, 2011; Randi et al., 2014) require an informed and effective management of the populations (Hindrikson et al., 2017). Management interventions may involve control of wolf populations through legal killings (Bradley et al., 2015; Harper et al., 2008; Santiago-Avila et al., 2018) or non-lethal management options (McManus et al., 2015; Treves et al., 2016) such as sterilization of breeders (Donfrancesco et al., 2019; Haight and Mech, 1997). In order to inform and help managers in making the best decisions, models are needed to forecast the impact of alternative management regimes on the dynamics and viability of the species (Bull, 2006; Marescot et al., 2013). Not only models can help selecting management strategies among several, they can also define the most effective application of a strategy in particular (e.g., its intensity, its frequency) (Haight and Mech, 1997).

Different types of models have been used to project the dynamics of highly social species. Stage-structured models including age-, breeding- or dispersing-specific individual categories have been developed to predict population growth rate hence relevant to make predictions at the population level (Haight and Mech, 1997; Marescot et al., 2012). Individual-based models

(IBMs) have also been used to model population dynamics and proven to be more flexible to represent species with complex social structure like wolf or coyote (Chapron et al., 2016; Marucco and McIntire, 2010; Pitt et al., 2003). IBMs are bottom-up models that simulate the fate of individuals interacting with each other and/or their environment. IBMs can include many individual-level mechanisms (i.e., behavioral rules) and therefore can represent complex individual interactions as exhibited by these social species (Chapron et al., 2016; Haight et al., 2002; Marucco and McIntire, 2010; Pitt et al., 2003). Population-level results emerge from the individual-level simulations (Railsback and Grimm, 2012). IBMs are modular models, in that they are built as series of sub-models. Sub-models represent either components of the life cycle of the species (e.g., reproduction sub-model, mortality sub-model) or external factors that modify the population structure (e.g., immigration sub-model, management sub-model). In this respect, IBMs can be very flexible as sub-models can be reorganized, removed or new ones can be added. This flexibility allows to mimic the species life cycle very closely, as well as testing the impact of external processes on the simulated population, such as different management actions (Bull et al., 2009; Hradsky et al., 2019). Chapron et al. (2016) used IBMs to estimate a conversion factor applied to the number of packs in order to estimate the total wolf population size in Scandinavia. Haight et al. (2002) used IBMs to simulate the impact of different wolf-removal strategies on depredation. Marucco and McIntire (2010) built a spatially explicit IBM to predict the wolf recolonization in the Italian Alps including the dispersal process and territory establishment of individual wolves accounting for the suitability of the landscape. Already including many processes affecting wolf dynamics, some individual behaviors and processes affecting pack structure and dynamics were omitted in these IBMs, thereby leaving room for further development.

The pack consisting of one breeding pair together with subordinates holding a territory is the basic social unit of a wolf population (Mech and Boitani, 2003). Individual behaviors and social dynamics leading to new pack formation or to dissolution of existing packs have an effect the overall population dynamics (Chapron et al., 2016). For example, Brainerd et al (2008) found that the loss of breeders might disrupt packs stability depending on pack size prior and whether one or none breeders remained. Borg et al. (2015) tested the impact of this mechanism on the growth rate of the saturated wolf population of Denali National Park and Preserve, Alaska and found that it had no significant effects on immediate or long-term population dynamics. However, they hypothesized that the influence of breeder loss in small, isolated or recolonizing populations may be greater. As another example, several studies observed that vacant male breeding positions were filled primarily by unrelated immigrants, while vacant female breeding positions were mostly filled by subordinates of the same packs (Caniglia et al., 2014; Jedrzejewski et al., 2005; Vonholdt et al., 2008) and suggested that these mechanisms are implied in inbreeding avoidance. Other observed social dynamics such as the adoption of unrelated individuals within packs and the different mechanisms of formation of reproductive pairs like "budding" (i.e., the establishment of a new pack with a subordinate from another pack) and pair bonding (Mech and Boitani, 2003) are linked to the availability of potential replacement breeders, and to formation of new packs. These individual behaviors, life-history traits and social dynamics, if not accounted for in models, may negatively affect conclusions of studies assessing population parameters such as genetics or inbreeding (Caniglia et al., 2014; Vonholdt et al., 2008), hybridization (Fredrickson and Hedrick, 2006) evaluating alternative management scenarios (Haight et al., 2002; Haight and Mech, 1997). Such wrong evaluation can potentially mislead management decisions and result in the failure of management actions.

Here we developed an IBM to project wolf dynamics that includes fine-scale individual and pack dynamics using the up-to-date scientific literature. Our model explicitly includes interactions between individual wolves, accounting for changes in wolf status (i.e., breeder vs subordinate, resident vs disperser) and dispersal processes while taking into account individuals' relatedness to mimic inbreeding avoidance. To highlight the flexibility and modularity of our IBM, we ran multiple versions of it. Specifically, we assessed the effects on the models' performance of removing, changing the composition or changing the order of some dynamics processes (i.e., sub-models), targeting processes usually not included in previous IBMs simulating wolf demography. To explore the effects of not considering aspects of social dynamics when projecting wolf population dynamics, we contrasted their predictions with those of the complete IBM in terms of the number of packs and their turnover, the number of individuals and their status, and the relatedness inside the breeding pairs. We developed our model using the R language to facilitate its understanding and easy access for modifications by ecologists. Therefore, given the flexibility of the model structure and its language, our IBM can be used by many ecologists, managers and practitioners and be adapted to their specific research questions and management issues on wolf, as well as species with similar social structure (e.g., coyote).

2. Methods

2.1. Wolf IBM

The model simulates the life cycle of the gray wolf using an individual-based structure, including fine-scale individual processes and pack dynamics. We focused the IBM structure on modeling the wolf internal dynamics, but did not make it spatially explicit. The model was calibrated mostly on wolf populations from central Europe (i.e., Alps, Apennines) but can easily

accommodate for others (e.g., North American populations) with a few modifications on the parameter values and the sub-models series (e.g., see *2.1.3.12. Pack splitting*). The complete description of the IBM following the Overview, Design concepts, and Details protocol ("ODD" protocol) (Grimm et al., 2010, 2006) is provided in Appendix A.

2.1.1. Initial population

The composition of the initial population needed to launch the IBM simulations as well as the model parameters pack carrying capacity, number of immigrants arriving per year and proportion of dispersing wolves emigrating are to be defined by the user to best represent the wolf population he/she wants to model. Here is a simple fictive example to show the model operation. We built an initial population of 10 packs and 5 dispersers, in an environment that can hold 30 packs in total (i.e., pack carrying capacity, Table 1, Appendix A). Specifically, the population comprised 5 packs of 2 breeders (5 years old each) with 2 pups (one male and one female); 3 packs of 2 breeders (5 years old each) with 1 yearling (male) and 1 pup (female); 2 packs of 2 breeders (5 years old each) with 1 adult (female, 3 years old); and 5 dispersers (3 females, 2 males, 2 years old each). We estimated the size of the area where the population was simulated as the pack carrying capacity multiplied by the average territory size for wolf populations in the Apennines (104 km^2) (Mancinelli et al., 2018). We allowed connections of the simulated population with other wolf populations (not simulated) via a fictive immigration of 0, 1 or 2 external wolves per year inside the simulated population and emigration of 0.1 % of the dispersing wolves from the simulated population outside of the study area.

2.1.2. IBM main structure

Simulated individuals represent wolves. Each one holds a unique ID, a sex (male or female), an age, if there are resident (i.e., inside a pack) or disperser, breeder or not, a pack ID (when they belong to a pack), their own genealogy (i.e., their mother ID and father ID), and their cohort ID.

Wolf age was defined as the year the wolves are living in (e.g., age 1 for pups of age 0 to 12 months) such as wolves of 1 are pups, wolves of 2 years of age are yearlings and wolves of ≥ 3 years are adults. We stated sexually mature individuals at ≥ 2 years (i.e., yearling and adults). Wolves belonging to the same pack have the same pack ID. A pack is defined by one breeding pair at most with several non-breeding subordinates. Because of the death of one or both breeders, a pack can stay without a breeding pair for a while. It can also be without any subordinate. For programming simplicity, we also considered that a solitary resident wolf holding a territory alone constitutes a pack. In this model, "dispersers" or "dispersing individuals" include all non-resident individuals, both those that are actually in a dispersal movement (i.e., leaving their natal pack and looking to establish a new one) as well as floaters (i.e., nomadic individuals not holding a territory, available to replace missing breeders in packs or to establish a new pack (Mancinelli et al., 2018)). Wolves do not have a precise location as this IBM is not spatially explicit. Instead, we considered their spatial distribution as indirectly represented through their pack affiliation because of the exclusive territoriality of the species.

The time step of the model is one year. Each year, all simulated individuals go through the same series of different sub-models representing different processes of the wolf life cycle, and each individual behaves differently according to its own characteristics. In order, these sub-models are: reproduction, aging, mortality, and change of status (Fig. 1). The change of the wolves' status encompasses several sub-models which, in order, are: pack dissolution, replacement of breeding females by subordinates, dispersal (within the simulated population), long-distance immigration/emigration (from/to outside of the simulated population), adoption, replacement of breeders by dispersers, new pack establishment in breeding pairs, new pack establishment by budding, new pack establishment alone, replacement of breeding males by subordinates (Fig. 1). Immigration of external wolves into the simulated population and

emigration of simulated wolves leaving the study area do not change the simulated wolves' status *per se*, as it introduces new unrelated individuals or remove locally born individuals from the population. However, this sub-model was included in the group of sub-models "change of status" (Fig. 1) because we placed immigration and emigration after dispersal to have dispersing individuals in the model to potentially emigrate. All sub-models are detailed below and their parameter values are listed in Table 1. Sub-models rules were defined to reproduce individual behaviors and pack dynamics as closely as possible to the reality. However, some processes hard to understand or poorly documented were represented as simple IBM rules to reproduce expected population outcomes.

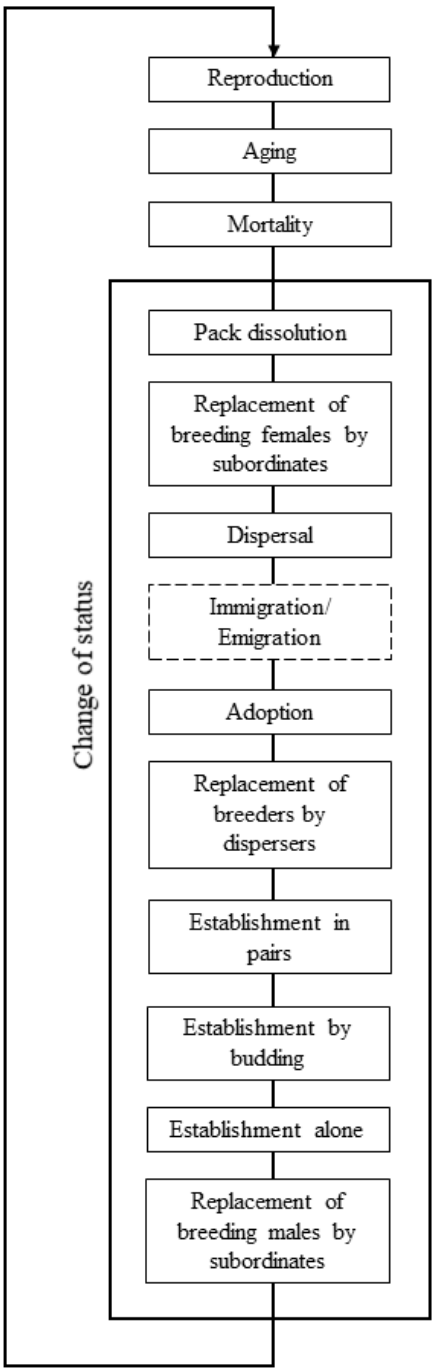


Figure 1: Diagram of the wolf individual-based model with the series of sub-models in order: reproduction, aging, mortality, and change of status. The change of the wolves' status varies step by step according subsequent sub-models from pack dissolution to replacement of breeding males by subordinates. Immigration/emigration (dotted box) does not change the wolves' status but

needs to follow the dispersal sub-model to update the pool of dispersing individuals. This loop of sub-models represents a one-year time step. Simulated wolves go through each sub-model of this loop, starting with reproduction, all wolves together, one sub-model at the time, for as long as the simulation lasts.

(1.5-column fitting image)

Table 1: Parameters used in the wolf IBM.

Parameter	**Sub-model in which the parameter is used (see Fig. 1)**	**Explanation**	**Value**	**Reference**
Mean litter size	Reproduction	Number of pups that goes out of the female den. Mean used for a Poisson distribution to generate the number of pups produced by a breeding pair.	6.1	Sidorovich et al. 2007
Pup mortality	Mortality	Mortality probability for wolves in their first year of their life.	0.602	Smith et al. 2010
Yearling mortality	Mortality	Mortality probability for non-dispersing yearlings.	0.18 (sd = 0.04)	Marucco et al. 2009

Non density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is not at pack carrying capacity.	0.18 (sd = 0.04)	Marucco et al. 2009
Density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is at pack carrying capacity. popDens is the population density per 1000 km2	1 - (1 / (1 + exp(-1.196 + (-0.505 * (popDens-53.833) / 17.984))))	Cubaynes et al. 2014
Pack carrying capacity	Mortality; Establishment in pairs; Establishment by budding; Establishment alone	Maximum number of packs the environment within which the population is simulated can hold.	30	Defined by the user
Territory size	Mortality	Average territory size (in km^2) for wolves. Used to calculate the study area size with the pack carrying capacity to estimate wolf density through the model	104	Mancinelli et all. 2018

Dispersing pup mortality	Mortality	Yearly mortality probability for individuals that dispersed as pups and were not adopted by a pack during their dispersal year.	1	
Disperser mortality	Mortality	Yearly mortality probability for dispersers (except individuals that dispersed as pups).	0.31	Blanco and Cortes, 2007
Dissolution probability for pack with 1 breeder	Pack dissolution	Probability of dissolution for small packs that have only 1 breeding individual left in the pack.	0.258	Brainerd et al. 2008
Dissolution probability for pack with 0 breeder	Pack dissolution	Probability of dissolution for small packs that do not have any breeding individual left in the pack.	0.846	Brainerd et al. 2008
Pack size threshold for dissolution	Pack dissolution	Pack size to differentiate large (5.75 individuals) and small (2.36 individuals) packs. Packs with less individuals than this threshold are considered	4.055	Brainerd et al. 2008

		smalls and can dissolve if only 1 or 0 breeding member remains.		
Relatedness threshold	Replacement of breeding females by subordinates; Establishment in pairs; Establishment by budding; Replacement of breeders by dispersers; Replacement of breeding males by subordinates	Relatedness value between 1st cousins. Two individuals must have their relatedness coefficient less or equal this threshold to mate.	0.125	Caniglia et al. 2014
Mean pack size	Dispersal; Adoption	Mean number of individual in packs. Mean used for the Normal distribution to generate the maximum number of individuals in each pack.	4.405 (sd = 1.251)	Marucco and McIntire, 2010

Pup dispersal probability	Dispersal	Probability for a pup to leave the pack and become disperser when there are too many individuals in the pack.	0.25	Haight and Mech, 1997
Yearling dispersal probability	Dispersal	Probability for a yearling to leave the pack and become disperser when there are too many individuals in the pack.	0.5	Haight and Mech, 1997
Adult dispersal probability	Dispersal	Probability for an adult to leave the pack and become disperser when there are too many individuals in the pack.	0.9	Haight and Mech, 1997
Number of immigrants	Immigration/ Emigration	Number of immigrants arriving in the population each year. All values have the same probabilities to be chosen.	0,1 or 2 (for our theoretical case studies)	Defined by the user
Proportion of emigrants	Immigration/ Emigration	Proportion of dispersing individuals that emigrate outside of the study area	0.1 (for our theoretical case studies)	Defined by the user

Probability of adopting	Adoption	Probability for a pack that has less member than its maximum pack size to adopt a young disperser.	0.5	
Probability of budding	Establishment by budding	Probability of success for a disperser to establish by budding. This probability is multiplied by the density-dependent probability of establishment for the dispersers.	0.5	

2.1.3. Wolf IBM sub-models

2.1.3.1. Reproduction

We simulated that all packs with a breeding pair reproduce each year (Marucco and McIntire, 2010). We defined the number of pups each pair produces by sampling values in a Poisson distribution (Chapron et al., 2016) of mean equal to 6.1 (i.e., number of pups emerging from the den; (Sidorovich et al., 2007)). The sex of each pup is randomly chosen as male or female with a 1:1 ratio (Marucco and McIntire, 2010; Sidorovich et al., 2007). Newborn pups are of age 0, as all individuals will go through the "aging" sub-model afterwards (Fig. 1). Pups are residents, with the pack ID of their parents. Their mother and father IDs are recorded, and pups obtain the cohort ID related to the current simulated year.

2.1.3.2. Aging

All individuals age one additional year in this sub-model. Pups of the year are now 1 year old, yearlings are 2 years old, and individuals ≥ 3 years enter the adult age class.

2.1.3.3. Mortality

Mortality causes (e.g., starvation, disease, collisions, culling, poaching, intraspecific strife) and rates differ among individuals according to their age (Marucco and McIntire, 2010), and their residential status (i.e., resident vs disperser) (Blanco and Cortés, 2007). Moreover, higher population densities cause competition for food, space and mates, and may also induce a higher adult mortality due to intraspecific aggressions (Cubaynes et al., 2014). We simulated 7 different mortality rates, according to various combination of age, dispersing status of the individuals, and total number of packs in relation to the pack carrying capacity. Mortality is applied individually using a Bernoulli distribution.

2.1.3.3.1. Mortality for non-dispersing individuals

All pups have a mean probability of 0.602 to die (Smith et al., 2010), whereas it is 0.18 (sd = 0.04) for non-dispersing yearlings (Marucco et al., 2009). We applied two different mortality rates for non-dispersing adults depending on the number of established packs in the population. If the number of established packs is below the pack carrying capacity, mortality is fixed and similar to those of the non-dispersing yearlings. However, if the number of established packs is equal to the pack carrying capacity of the area, mortality is density-dependent. We used the equation linking wolf survival (φ) with wolf density from Cubaynes et al. (2014) to estimate the density-dependent mortality for non-dispersing adults: $\text{logit}(\varphi) = 1.196 + (-0.505 * \text{popDensStd})$, where popDensStd is the standardized wolf density per 1000 km2 with mean and standard deviation values equal to 53.833 and 17.984 respectively. Wolf density is calculated as the total number of wolves, without considering the pups, divided by the area where the population is simulated.

2.1.3.3.2. Mortality for dispersing individuals

At that stage, no pup can be dispersing (see the order of the sub-models, Fig. 1). Current dispersing yearlings are individuals whose pack dissolved (i.e., broke down) when they were still pups during the previous year and which were not adopted by an existing pack during that year (otherwise they would be residents). We assumed that these individuals were too young to survive by themselves a whole year without a pack, if not adopted, so we set their mortality probability equal to 1. Dispersing adults have a mortality probability equal to 0.31 (Blanco and Cortés, 2007).

2.1.3.3.3. Mortality for old, non-dispersing and dispersing, individuals

We did not model senescence or any increase of the mortality probability with age. To represent realistic age distribution in the population, the limit for wolves is the end of their 15th year of simulation (Marucco and McIntire, 2010) and all individuals reaching 16 years old die.

2.1.3.4. Pack dissolution

Packs whose social structure have been impacted by the loss of one or both breeders may break down. Small packs (up to 4 individuals) with one remaining breeder may dissolve with a probability of 0.258, whereas packs where no breeder is left dissolve with a probability of 0.846 (Brainerd et al., 2008). In the specific case where both breeders died and only pups remain, we defined that the pack always breaks down as we assume pups alone are unlikely to maintain a territory by themselves without parental care. These pups are considered as dispersing as they do not belong to a pack anymore. Their survival alone is low without food or care from adults or yearlings (Brainerd et al., 2008; Mech and Boitani, 2003) but they can be adopted by another pack during the current year. If they do not, we assume they die in the mortality sub-model in the next time step. When a pack dissolves, all former members of the pack become dispersers and do not belong to a pack anymore. Former breeding individuals then lose their status.

2.1.3.5. Replacement of breeding females by subordinates

When a breeding female dies in a wolf pack, she is most likely replaced by one of the subordinate females in the pack (most likely one of her daughters) (Caniglia et al., 2014; Jedrzejewski et al., 2005; Vonholdt et al., 2008). Combined to this, there is a general avoidance of inbreeding in wolf packs (Caniglia et al., 2014; Vonholdt et al., 2008). We simulated the replacement of a missing breeding female in a pack by randomly choosing one among the subordinate mature females. Once the new breeding female is chosen we look at the relatedness between her and the current breeding male, if there is any. If there is a breeding male in the pack and he is too closely related to the chosen female, he may be replaced (in following sub-models *2.1.3.9. Replacement of breeders by dispersers* and *2.1.3.14. Replacement of breeding males by subordinates*) by a disperser or a less related subordinate from the pack who will usurp the established breeding position (Mech and Boitani, 2003). The relatedness threshold chosen is the one of the first cousin ($r = 0.125$); a mating pair of breeding wolves can be cousins but hardly more related than this except when wolves have no other option (e.g., no mating between siblings or parents and children when possible) (Caniglia et al., 2014). This relatedness threshold is the same for all the following sub-models. This sub-model runs before the dispersal event to prevent subordinates, which will potentially replace the breeding female, to leave the pack.

2.1.3.6. Dispersal

Wolves routinely disperse in response to competition and aggression related to food availability and breeding opportunity within their pack (Mech and Boitani, 2003). Non-breeding wolves are pushed to leave the pack because of social drivers limiting the group size within the territory (Ballard et al., 1987; Fritts and Mech, 1981; Fuller, 1989; Gese and Mech, 1991; Mech, 1987). In areas of high prey availability, dispersal is postponed (Ballard et al., 1987; Blanco and Cortés, 2007; Jimenez et al., 2017) and is rather triggered by the onset of sexual maturity of young

wolves (Gese and Mech, 1991; Messier, 1985; Packard and Mech, 1980) so that most wolves have dispersed from their natal pack by the age of 3 (Gese and Mech, 1991; Jimenez et al., 2017). For each pack, and at each time step, we simulated the maximum number of individuals that the pack can support using a Normal distribution with a mean pack size of 4.405 wolves (sd = 1.251, (Marucco and McIntire, 2010)). If the pack exceeds the threshold, some individuals have to leave the pack until the number of wolves in the pack equal the threshold. While breeding individuals cannot disperse, all the other wolves can disperse with probabilities related to their age: pups may disperse with a probability of 0.25, yearlings with a probability of 0.5, and adults with a probability of 0.9 (Haight and Mech, 1997).

2.1.3.7. Immigration/Emigration

Given wolves dispersal abilities, individuals may move from one population to another through long distance dispersal (Blanco and Cortés, 2007; Ciucci et al., 2009). For the immigration part, at each time step, a determined number of immigrants enters the population. The sex of the immigrants is random (i.e., male or female with a 1:1 ratio). Their age is simulated using a truncated Poisson distribution of mean equal to 2 (with boundaries between 1 and 15) as the most common age class of dispersers is the one of yearlings (Mech and Boitani, 2003). Immigrants are simulated as dispersers, generated from another wolf population. They do not belong to any pack of the simulated populations yet, and consequently are not breeders. As they were born outside the simulated population, they do not hold information about their mother ID and father ID. However, immigrant wolves will behave the same way (i.e., follow the same sub-model rules) as the native wolves. For the emigration part, a proportion of the current dispersing individuals, randomly chosen, leave the simulated population. These individuals will not come back and their disappearance is similar to simulating their death.

2.1.3.8. Adoption

Young lone wolves not holding a territory sometimes join and are adopted by packs that already have a breeding pair (Mech and Boitani, 2003). Most adoptees are males of 1 to 3 years old and most adoption events take place from February through May (Meier et al., 1995; Messier, 1985). We did not find an estimate for adoption probability so we arbitrary set to 0.5 the probability to adopt dispersing individuals, for packs whose size is below the maximum threshold (estimated in the dispersal sub-model). These packs can adopt as many individuals between 1 and 3 years old (included) as allowed by their maximum pack size. Among potential adoptees, dispersing males are selected first. If there are no more males and still packs available for adoption, then dispersing females are chosen next. Once dispersers have been adopted, they become residents and belong to the pack as non-breeding members (i.e., subordinates).

2.1.3.9. Replacement of breeders by dispersers

Genetic studies found that vacant male breeding positions are mostly filled primarily by unrelated individuals (Caniglia et al., 2014; Jedrzejewski et al., 2005; Vonholdt et al., 2008). Here, we simulated the replacement of all missing breeders by mature dispersers, comprising both missing breeding females that could not be replaced by a subordinate at an earlier time in the model (*2.1.3.5. Replacement of breeding females by subordinates*) and missing breeding males. Missing breeding females are replaced by mature dispersing females, unrelated to the current breeding males of the packs if there are any to avoid inbreeding (Caniglia et al., 2014; Vonholdt et al., 2008). Selected females become breeders of their assigned pack, change their status to residents, and belong to the pack they integrated. After that, the same is done for the packs missing breeding males with mature male dispersers filling the positions, selected among genetically unrelated individuals that will mate with the breeding females of the packs if there are any. If there are packs where the missing breeding female was replaced by a subordinate (in *2.1.3.5. Replacement of breeding females by subordinates*) and the current breeding male was too related

to her, the same is done for these packs with unrelated mature male dispersers usurping the established male breeders (Mech and Boitani, 2003). The breeding males replaced by dispersers are dismissed from their position and become subordinates in their own pack.

2.1.3.10. Establishment in pairs

One of the main mechanisms for dispersing wolves to reproduce is to form a new pack, first with another dispersing mate of opposite sex (Mech and Boitani, 2003). In the IBM, male and female dispersers can pair bond, establish together as breeders, and form a new pack (only mature dispersers that are not too closely related can do so). However, this is possible only if the number of existing packs has not reached yet the maximum allowed by the pack carrying capacity of the area. Given this condition, the density-dependent probability for dispersers to pair bond is defined by a Bernoulli distribution with probability equal to the number of packs that can be created divided by the pack carrying capacity in packs of the area (i.e., the more packs, the less chance for dispersers to pair bond and establish a new pack). Once a pair bond is established between mature dispersing male and female, they both become breeders, residents and obtain the same, new and unique pack ID.

2.1.3.11. Establishment by budding

Another breeding strategy for dispersing wolves is to pair with a mature subordinate wolf from an existing pack that did not disperse and establish a new pack of their own (i.e., called “budding”) (Brainerd et al., 2008; Mech and Boitani, 2003). Similar to the establishment in pairs, it is possible only if the number of packs has not reached the pack carrying capacity. The probability for a disperser to bud is the density-dependence probability for establishment in pairs times a probability to bud equal to 0.5. We defined arbitrary this 0.5 factor to make budding less likely than forming a new pack in pairs. Only mature dispersers can bud, and only with a non-breeding mature resident of the opposite sex that is not too closely related. Once there is a match between a

disperser and a subordinate wolf to bud, they both become breeders, residents and obtain the same, new and unique pack ID.

2.1.3.12. Pack splitting

Splitting is another strategy for wolves to form new packs and reproduce. A subgroup of individuals permanently splits off from their original pack to form a new one nearby, often due to presence of two breeding pairs in the pack (Mech and Boitani, 2003). It differs from budding in that no dispersing individual is involved in the process. Recorded pack splitting involved large packs, mainly in North American wolf populations (Hayes and Harestad, 2000; Jedrzejewski et al., 2004; Meier et al., 1995; Vonholdt et al., 2008). We did not consider such phenomenon in our IBM as pack sizes in central Europe are much smaller and multiple breeding pairs are less likely to occur (Caniglia et al., 2014; Marucco and McIntire, 2010). To simulate North American wolf populations, this sub-model should be added as a new type of pack establishment.

2.1.3.13. Establishment alone

Finally, dispersing individuals can establish a new territory by themselves, waiting for a mate to later join them (Wabakken et al., 2001). If the area is not at pack carrying capacity, we considered in the IBM, that remaining mature dispersers which could not establish themselves in pairs or by budding can establish a territory alone. The probability to establish alone is also density-dependent (same as for the establishment in pairs) and the individuals become breeders (even if no reproduction is possible yet) and residents their new pack, obtaining a new and unique pack ID. Then, a mature disperser of the opposite sex will be able to take the vacant breeding position at the next time step (in the sub-model *2.1.3.9. Replacement of breeders by dispersers*) to become a breeding pair that reproduce.

2.1.3.14. Replacement of breeding males by subordinates

When no mature male disperser could replace the missing breeding male in a pack, one of the subordinates can take over. If there are several mature male subordinates in the pack, the choice is done among the least genetically related to the current breeding female. If there are several available subordinate males, or if there is not any breeding female, the choice among the potential breeders is random. If the breeding female is too related to the newly chosen breeding male and there is a mature female subordinate less related, she will become breeding female and the current breeding female is dismissed (i.e., becomes subordinate). If there are several mature female subordinates least related, the choice among them is random. If the current breeding female is less or equally related to the breeding male than the mature female subordinates, she maintains her breeder status. In the particular case where there was a missing breeding female replaced by a subordinates (in *2.1.3.5. Replacement of breeding females by subordinates*) and the current breeding male was too related to her, one of the male subordinates can take over the male breeding position, only if there is a male subordinate less related to the breeding female than him. If not, the breeding male keeps his position, mimicking the fact that wolves change partner to avoid incest, except when there is no better alternative (Mech and Boitani, 2003). Once new breeding individuals are chosen, they will be able to mate the next year.

2.1.4. Implementation

The model was coded in R 3.5.2 (R Core Team, 2014). Our aim was to make this model useful for ecologists who could adapt the IBM for their own specific research and management applications. The R language is largely used by ecologists and coding the model in this language should likely ease its understanding and adaptation. We used the R package NetLogoR (Bauduin et al., 2019) to facilitate the implementation of the individual-based model structure in R language and the package pedantics (Morrissey, 2018) to calculate relatedness between

individuals using their mother and father IDs. We also used the packages SciViews (Grosjean, 2018) and testthat (Wickham et al., 2019). The R files to run the model are described in Appendix B.

2.2. Different sub-model series

Some of the sub-models we integrated in our IBM represent aspects of wolf dynamics that were incorporated in a different order, or were not included at all, in other wolf IBMs (Chapron et al., 2016; Haight et al., 2002; Marucco and McIntire, 2010; Pitt et al., 2003). We assessed our model performance and sensitivity to these processes by running and comparing different versions of the wolf IBM whether by cancelling or moving one sub-model at the time (Fig. 2). We removed the sub-models of pack dissolution (Model M1, Fig. 2), adoption (M2, Fig. 2), establishment by budding (M3, Fig. 2) and immigration/emigration (M4, Fig. 2). We also changed the order of sub-models in the wolf life cycle by considering first breeder replacement by subordinates for both sexes and then by dispersers (M5, Fig. 2), as well as the other way around (M6, Fig. 2). Finally, we removed some of the mechanisms in the model by modifying some parameter values. Specifically, we removed the avoidance of inbreeding in wolf packs by setting the relatedness threshold to its maximum value (M7) (i.e., any pair, such as parent-child or brother-sister could mate). We also removed the density-dependent mortality for the adult residents when the population was at pack carrying capacity by setting mortality rate to 0.18 for the whole simulation (M8). For each of the 8 models described above, as well as for the original model (M0), we ran 200 replicates for a 25-year simulation period starting with the same initial population.

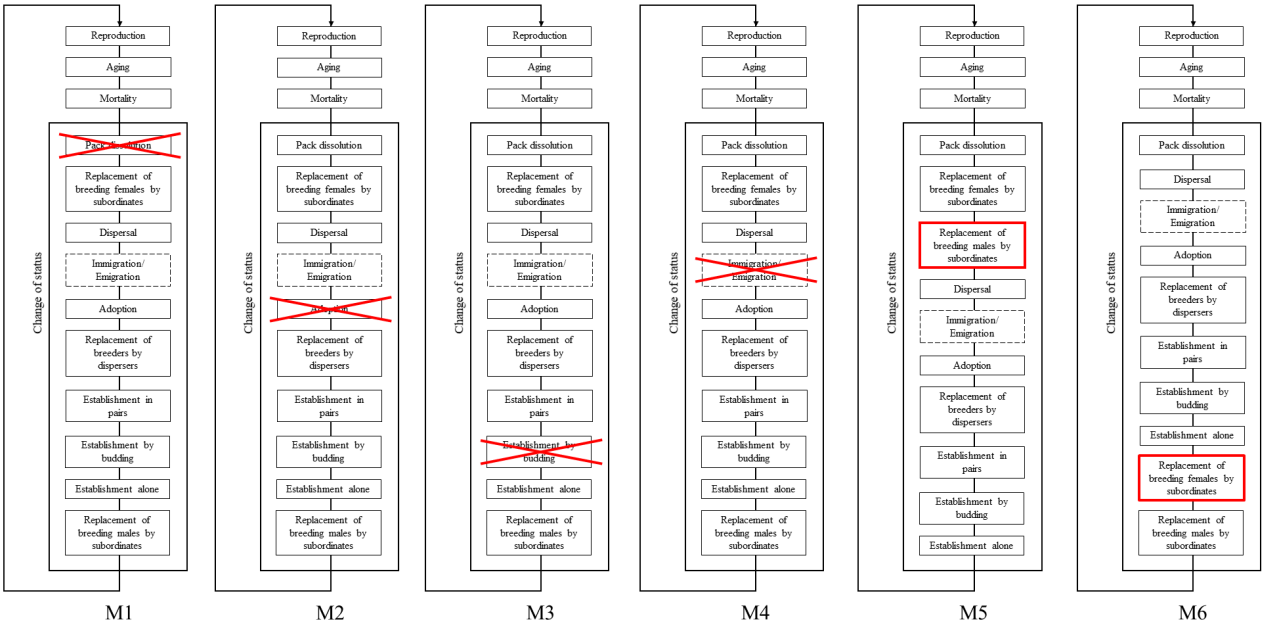


Figure 2: Different sub-models series tested for the wolf individual-based model. In models M1 to M4, we removed one of the sub-models (red cross), and in model M5 and M6, we changed the position of one sub-model (red rectangle). Models M7 and M8 are not presented as the sub-models series are not affected, only parameter values are.

(2-column fitting image)

2.2.1. Model outputs

For each simulation, the complete population with the individual's characteristics was available for each simulated year. The change in pack numbers (i.e., the number of packs lost and new ones created) was also recorded after each event modifying their number: mortality, pack dissolution, and the three types of new pack establishments. We considered 5 outcomes that represent metrics that may be crucial to decision maker for wolf conservation and management. Results represented the population at the last year of simulation and the variation around the mean value represented the variation among the 200 simulation replicates. We looked at 1) the number of

packs with a breeding pair. This metric is linked to the reproductive potential of the population and is of importance for management issues related to population growth. 2) The number of new packs formed during the year. This represents the pack turnover and the stability of the population that may affect wolf-human conflicts. 3) The number of individuals with 4) the proportion of residents and dispersers in the population. Population size is often required in management control and knowing the distribution of the resident/dispersing status of the individuals may help understanding the population behavior. Finally, we looked at 5) the relatedness between the two breeders in each pack. Inbreeding avoidance plays a big part in the wolf life cycle, affecting the replacement of the missing breeders and the creation of a new pack.

2.3. Sensitivity analysis

We ran the original complete version of the model (M0) modifying one parameter value (Table 1) at a time. We increased and decrease the focused parameter value of 5% and run 200 replicates of 25 years simulations (Ovenden et al., 2019). The model was considered sensitive to a parameter if a model output (i.e., mean value over the 200 replicates) with the one modified parameter varies more than 20% from the original results (Kramer-Schadt et al., 2005; Ovenden et al., 2019). We examined the model outputs described above in the *2.2.1. Model outputs* section. We did not test the sensitivity of the model to standard deviation parameters (standard deviation of mortality and of pack size, Table 1). Regarding the density-dependent mortality function, we only tested the sensitivity of the slope parameter and did not test the sensitivity to the intercept and the parameters to standardize the population density (Table 1).

3. Results

3.1. Wolf individual-based model

The original version of the IBM (M0) predicted a growth of the simulated wolf populations, starting from the initial population of 10 packs and 43 individuals up to a mean number of packs with a breeding pair equal to 29.3 (sd = 0.8) and 186.7 individuals on average (sd = 11.9) at the 25th year of simulation (Figs. 3.a, 3.b, 4.a, and 4.b). The populations reached pack carrying capacity and stayed stable after about 13 years of simulation (Figs. 3.a and 3.b), but on average, 2.1 packs (sd = 1.7) were formed during the last year of the simulation period (Fig. 4.c). Among the simulated individuals at the 25th year, on average 71% (sd = 4.7%) of them were resident and 29% (sd = 4.7%) were dispersers (Fig. 4.d). In packs with a breeding pair, the mean relatedness between the two breeding individuals was equal to 0.06 (sd = 0.03) (Fig. 4.e).

3.2. Different sub-model series

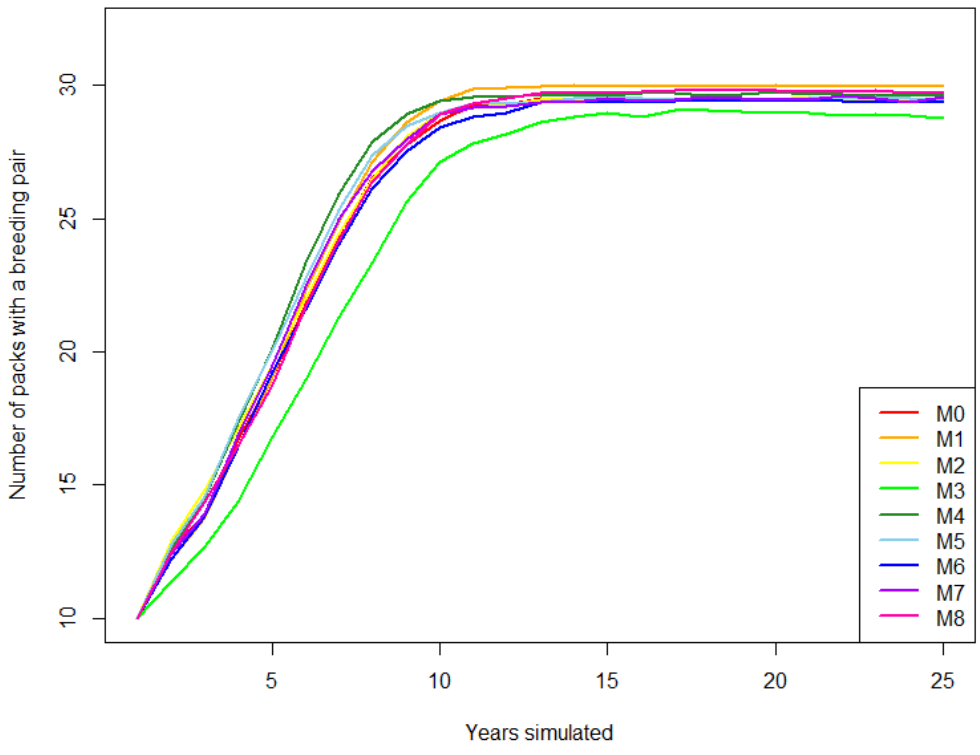
All modified versions of the model simulated populations with a similar growth as with M0 (Figs. 3.a and 3.b). They all reached pack carrying capacity at a similar time in the simulation, however M4 (i.e., no migration) had a faster growth than the others, and M3 (i.e., no establishment by budding) a slower one (Fig. 3.a). At the 25th year of simulation, all models had simulated populations with a number of packs having a breeding pair reaching pack carrying capacity (Fig. 4.a). Models M2 (i.e., no adoption), M4, M5 (i.e., replacement of breeding male by subordinates before than by dispersers), M6 (i.e., replacement of breeders by dispersers before than by subordinates) and M7 (i.e., no relatedness threshold) had population projections the most similar to those of M0. There was less variation in pack numbers, among the different replicates, in populations simulated by M1 (i.e., no pack dissolution) and M8 (i.e., no density-dependent adult mortality), with more simulations predicting a population at pack carrying capacity than M0. On the other hand, outputs from M3 had a much larger variation than the outputs from M0; a fewer replicates simulated populations reaching pack carrying capacity.

The growths of the populations in terms of number of individuals were similar to those for the pack numbers (Figs. 3.a and 3.b). There was also no large differences in number of individuals at the 25th year of simulation between model scenarios (Fig. 4.b) with similar variation in their outputs. However, models M1, and especially M4 and M8 simulated more individuals in the population than the other models.

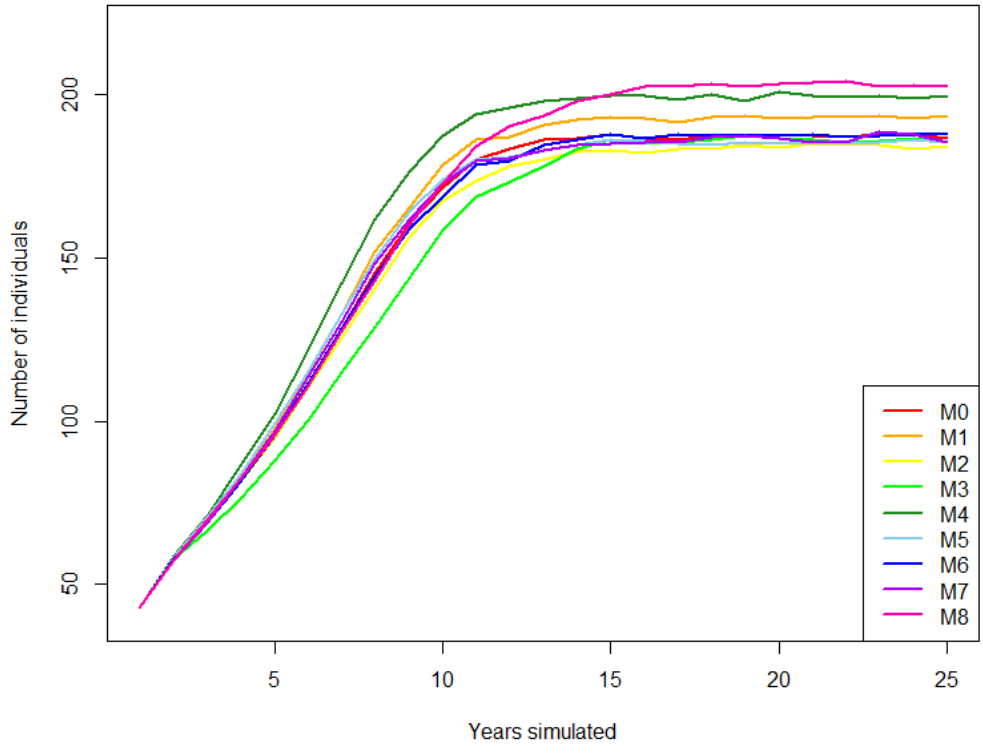
Regarding the number of new packs created during the 25th year of simulation (Fig. 4.c), all models, except M1, had similar outputs. Models M3 and M8 had a few less packs produced than in simulations done with M0, and M4 and M7 had a few more. M1 never simulated a new pack formation during the 25th year of simulation over the 200 replicates.

Models M2, M4, M5 and especially M8 produced on average less residents in the populations, and therefore more dispersing individuals, than M0 (Fig. 4.d).

Finally, the relatedness coefficient between the breeders in packs was the model output with the greatest differences among the models (Fig. 4.e). All models had very similar outputs with small values of relatedness between the breeders, except for model M5 and M7. These models simulated populations where the relatedness between breeders was more variable and much higher on average than M0, these differences being the greatest for M5 outputs.



a)

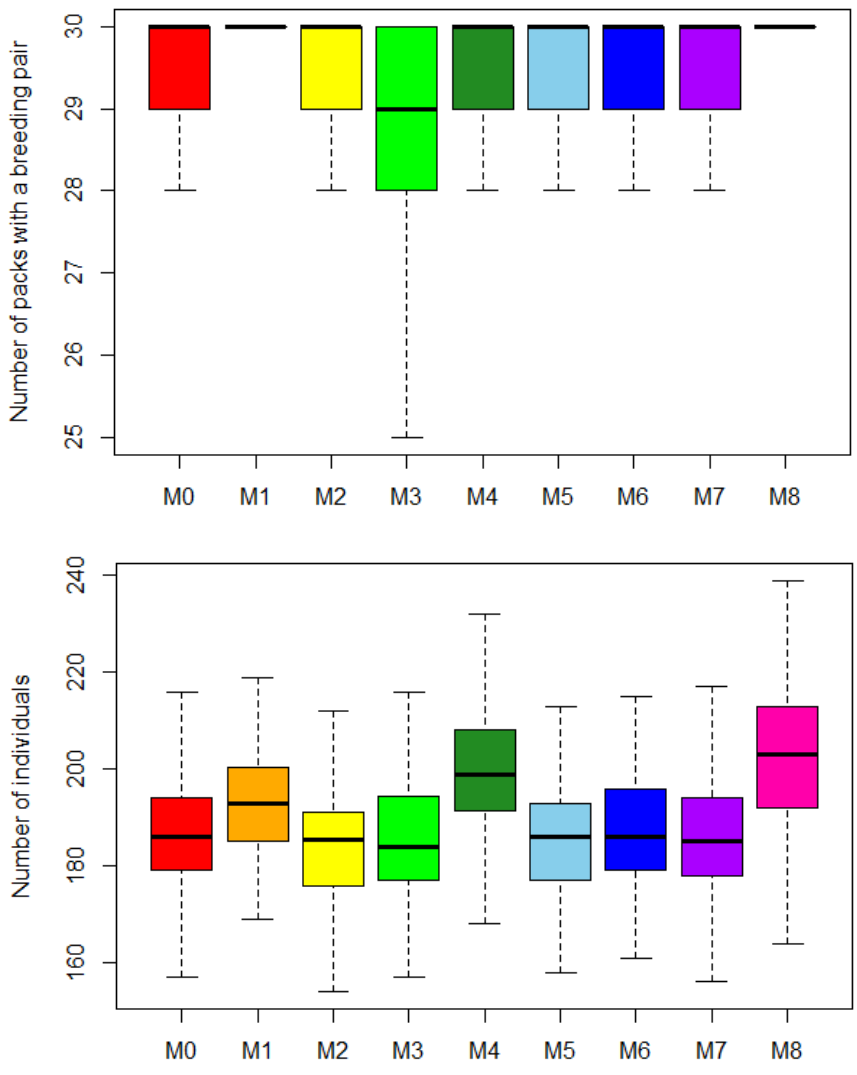


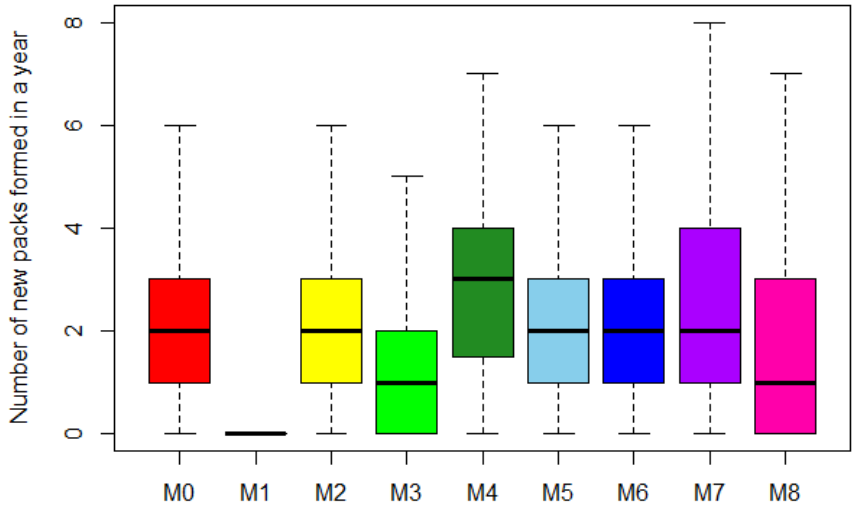
b)

Figure 3: Mean number of a) packs with a breeding pair and b) individuals predicted over the 25 years of simulation. The mean values were calculated over the 200 replicates of each model. M0

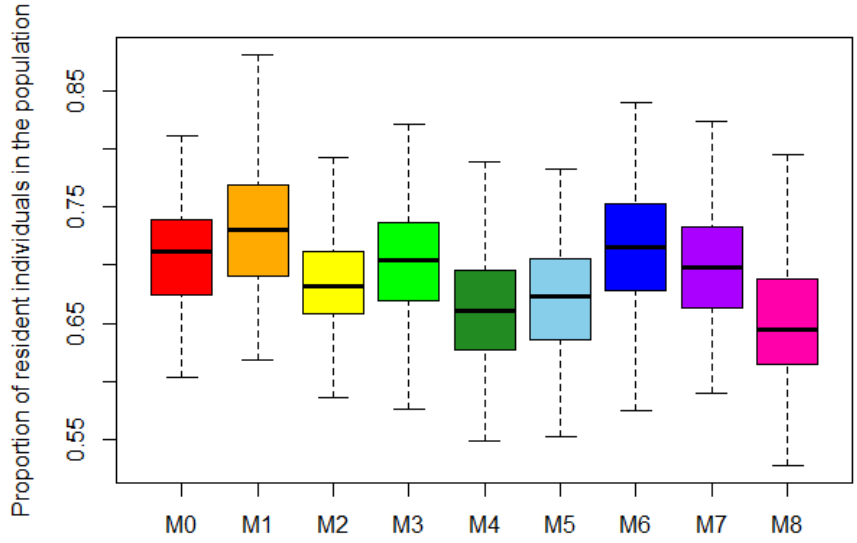
represents the original complete version of the model (Fig. 1) and models M1 to M8 represent the modified versions (Fig. 2). See figures 4.a and 4.b for the variances associated with the mean values for the 25th year of simulation.

(1.5-column fitting image)

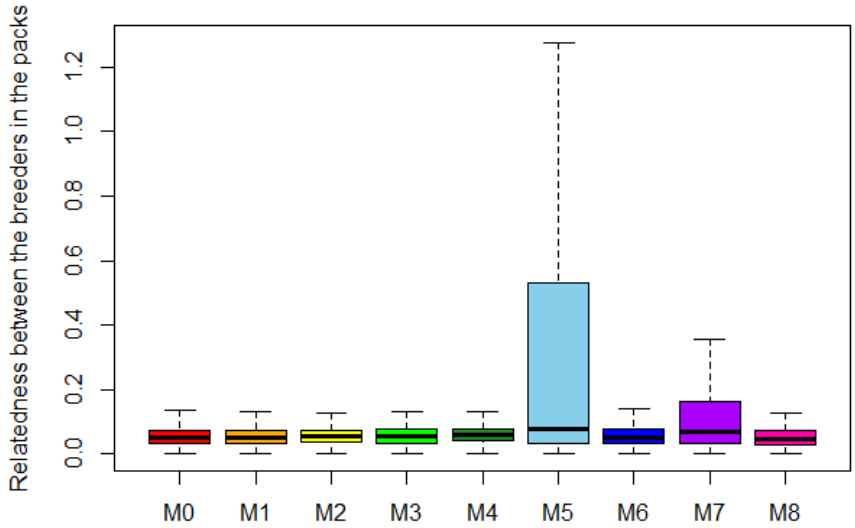



Number of new packs formed in a year
0
2
4
6
8
M0
M1
M2
M3
M4
M5
M6
M7
M8

c)


Proportion of resident individuals in the population
0.55
0.65
0.75
0.85
M0
M1
M2
M3
M4
M5
M6
M7
M8

d)


Relatedness between the breeders in the packs
0.0
0.2
0.4
0.6
0.8
1.0
1.2
M0
M1
M2
M3
M4
M5
M6
M7
M8

e)

Figure 4: Box plots of the 5 model outputs extracted at the end of the 25th year of simulation. The variation around the median represents the variation in the results among the 200 replicates due model stochasticity. a) Number of packs with a breeding pair. b) Number of individuals. c) Number of new packs created during the year through the different kind of new territory establishment. d) Proportions of resident individuals in the population. e) Relatedness between the male and female of the breeding pairs. M0 represents the original complete version of the model (Fig. 1) and models M1 to M8 represent the modified versions (Fig. 2).
(1.5-column fitting image)

3.3. Sensitivity analysis

As expected, the parameter affecting the most model outputs was the pack carrying capacity. The number of new packs created and the relatedness between breeders in packs were sensitive to this parameter. The number of packs created, the number of individuals and the proportions of residents and dispersers were not particularly sensitive to the pack carrying capacity, at least not in the range of [- 20%; + 20%]. The number of new packs created was more sensitive to the pack size threshold involved in the pack dissolution process and to the probability of adopting. The relatedness between breeders in packs was sensitive to the relatedness threshold.

Overall, the 5 model outputs we looked at were not very sensitive to the model parameters. Among the 21 parameters tested, increasing or decreasing the value of 17 of them did not modify the value of the results larger than their range [- 20%; + 20%]. The complete table with the value tested for the parameters and the results of the five outputs for each simulation run is available in Appendix C.

4. Discussion

Our work aimed at representing wolf demography and pack dynamics as best as possible using individual rules mimicking the wolf social behaviors. To do so, we developed an IBM which modularity and flexibility offer the possibility to be used and adapted by ecologists to explore various issues on wolf management, conservation and ecological understanding. Its individual-based structure allows studying theoretical questions about wolf ecology by including contrasted individual behaviors (e.g., mate choice; (Hedrick et al., 2016)), and the analysis of model predictions at the individual level to inform management and conservation strategies while acknowledging the species social structure.

Among the different sub-models series we tested, most led to inferences that were different from the original model (M0) we defined. As expected, ignoring pack dissolution (M1) produced a lower pack turnover with the population always being at pack carrying capacity with no new pack created. The only way a pack can disappear in the populations simulated with the model M1 is if all members of the pack die at once, which never happened in the simulations. As no pack disappears, once the population reaches pack carrying capacity, it stays there with no possibility for new pack to be formed. While it does not seem to modify the model predictions at the population level (i.e., number of packs or individuals), it has an effect on the individual composition with a population very stable. Similarly, Borg et al. (2015) showed that, with or without pack breaking down following breeder losses, the overall dynamics of the population was quite similar, enhancing the wolf social interactions compensation mechanisms. In contrast, not including density-dependent mortality (M8) also predicted populations systematically at pack carrying capacity but still with some pack turnover. The replacement of missing breeders in packs and the establishment of new packs was faster in this configuration (i.e., happened the same year as packs disappeared) with more individuals available as well as more dispersers in proportion than in the original model. The places left by the dissolved packs were filled right away by

available individuals. Therefore, if pack carrying capacity is always reached in both cases, it is not due to the same process: thanks to pack stability for M1, and faster breeder replacement in M8.

Model without immigration and emigration (M4) present similarities with M8: a high pack turnover and more individuals with more dispersers in proportion than simulated with M0. The immigration and emigration parameters seem to favor the departures of local dispersers rather than the entry of outsiders into the population as wolf dynamics is slowed down with the immigration/emigration process included (M0 vs M4). The strength of this process, and more generally of most of those studied with the 8 different model versions, also depends on its parameter values. For example, immigration/emigration may have a larger effect if more immigrants are allowed to enter the population or if more emigrants leave the study area. Rather than being an inconvenient, flexibility of parameters and initial population is an asset of this IBM because it allows ecologists to adapt the model to best represent their population of interest.

The model which does not include the process of new pack establishment by budding (M3) is the least likely to simulate populations reaching pack carrying capacity. As expected, removing a process to create a new pack does not change the population composition (i.e., number of individuals, proportion of residents and dispersers and relatedness) but decreased the possibilities for wolves to form packs. Pack turnover is also lower.

Having the replacement of the missing breeding female by a subordinate before a disperser has been documented in some study sites (Caniglia et al., 2014; Jedrzejewski et al., 2005; Vonholdt et al., 2008) but is debated. The modified model version where the replacement of the missing female breeder is done by a disperser before a subordinate (M6) produced model outputs very similar to those from M0. Either the type of individual replacing the missing breeding female has a low impact on the wolf dynamics, or this process may affect aspects of the

wolf population that we did not account for within the five metrics we considered to summarize the model predictions. However, the modular and flexible construction of the model allows future users to organize the replacement of the missing breeding females by the different type of individuals, as well as any other sub-models, in the order best representing their population of interest or the latest findings in literature.

Removing the adoption process (M2) predicted a higher proportion of dispersers than M0, as young wolves cannot be adopted by packs and remained floaters in the population (i.e., considered as "dispersers" in the model). Positioning the breeder replacement by subordinates before the replacement by dispersers (M5) also produced more dispersers, as they are not picked first for male breeder replacement. More interestingly, this modified version of the model favored inbreeding even more than the model without inbreeding avoidance process (M7). If we consider a breeding pair related when their relatedness coefficient is larger than 0.125 (Caniglia et al., 2014), only 0.2% of the breeding pairs were related in populations simulated with M0. In contrast, 39% of the breeding pairs were related in populations simulated by the model M5 and this proportion was equal to 30% for the model M7. These two results are way above the proportion of 7% found by Vonholdt et al. (2008) in the Yellowstone grey wolf population. These two model versions could likely bias results in hybridization and inbreeding studies with potential detrimental management recommendations for small isolated populations. This highlight the importance of considering these two processes in modeling wolf dynamics. However, the 0.2% of related breeding pairs estimated with the original model is surprisingly low compared to the field data from Yellowstone. Some elements may be missing in our original model to better reproduce the inbreeding process happening in the wild.

One of the limitations of our IBM approach is that it is non-spatial. This simplifies the use and adaptation of the model to other populations as no animal-environment interactions are

modeled and therefore no data regarding these interactions, which are sometimes hard to acquire, are needed. However, parameters like pack carrying capacity, territory size, number of migrants and proportion of emigration that need to be defined by the user is one way to account for spatiality constraints given by a particular environment as these parameters can be changed to best represent the study area of interest. But we agree that an explicit spatial mechanism would be very interesting to implement as wolf pack occupancy is mainly driven by exclusive territoriality (Cassidy et al., 2016). To add more spatial constraints without changing the model structure, a new individual characteristic could be defined to represent distances between individuals regarding their pack affiliation. Individuals from the same pack being closer to each other than from other individuals and therefore having the possibility to define small-distance dispersers vs long-distance dispersers (Louvrier et al., 2018), different from the immigration/emigration process of our model. With a bit of more work, the model could be turned into a spatially explicit IBM by including an explicit dispersal sub-model like in Marucco and McIntire (2010) in place of the current dispersal sub-model thanks to the modularity of our IBM structure.

Model outputs were sensitive only to a few parameters. Pack carrying capacity surely affected the model predictions as this parameter represents, as stated above, one of the main spatial constraint influencing the simulated population. Some of the impacting parameters are easier to obtain from field data (i.e., relatedness threshold (Caniglia et al., 2014; Vonholdt et al., 2008)) and their estimate were better known than others which are more complicated to estimate (i.e., pack size threshold for pack dissolution and probability for a pack to adopt a young disperser). In particular, adoption probability was arbitrary defined, due to a lack of estimate in the literature, and 0.5 can seem high for some populations where this event is limited. This parameter value influenced the number of new packs created and could change the whole population dynamics predictions if the real value appears to be much lower. More investigations

on the wolf population of interest are needed to obtain a better estimate of this parameter that can then be easily updated in the IBM.

With the complete IBM, we aimed at including all biological mechanisms documented in the literature to best represent the wolf life cycle. Overall, we hope that our reproducible implementation of a modular and flexible IBM will contribute to the management and conservation of wolf populations by providing a decision-making tool for stakeholders, as well as provide a base model to be adapted to simulate other canids and social species. The modular structure allows the modification of only specific components of the model while keeping the other sub-models and the main structure the same. Keeping in mind that removing or modifying some of the biological mechanisms produce different wolf population dynamics, as highlighted by our study. Coding the model in R will also likely facilitate the understanding, appropriation and adaptation of the models by ecologists. We used the R package NetLogoR to implement the individual-based structure that provides classes and multiple functions to easily code individual behavioral mechanisms. Modifications of the model (e.g., change in the existing sub-models, creation of new ones, etc.) can be done using this package to represent new processes and incorporate them in the IBM.

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7. References

Ballard, W.B., Whitman, J.S., Gardner, C.L., 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98, 54.

Bauduin, S., McIntire, E.J.B., Chubaty, A.M., 2019. NetLogoR: a package to build and run spatially explicit agent-based models in R. Ecography (Cop.). 42, 1841–1849. https://doi.org/10.1111/ecog.04516

Blanco, J.C., Cortés, Y., 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. J. Zool. 273, 114–124. https://doi.org/10.1111/j.1469-7998.2007.00305.x

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. J. Wildl. Manage. 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. J. Wildl. Manage. 72, 89–98. https://doi.org/10.2193/2006-305

Bull, J., 2006. A population viability analysis for wolves in Norway under different management regimes. Imperial College London.

Bull, J., Nilsen, E.B., Mysterud, A., Milner-Gulland, E.J., 2009. Survival on the border: a population model to evaluate management options for Norway's wolves Canis lupus. Wildlife Biol. 15, 412–424. https://doi.org/10.2981/08-010

Caniglia, R., Fabbri, E., Galaverni, M., Milanesi, P., Randi, E., 2014. Noninvasive sampling and genetic variability, pack structure, and dynamics in an expanding wolf population. J. Mammal. 95, 41–59. https://doi.org/10.1644/13-mamm-a-039

Cassidy, K.A., Smith, D.W., Mech, L.D., Macnulty, D.R., Stahler, D.R., Metz, M.C., 2016. Territoriality and inter-pack aggression in gray wolves: shaping a social carnivore's life history, in: Yellowstone Science: Celebrating 20 Years of Wolves. Yellowstone Science, pp. 37–42.

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., Balečiauskas, L., Balys, V., Bedõ, 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., Potoečnik, 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

(80-.). 346, 1517–1519. https://doi.org/10.1126/science.1257553

Chapron, G., Wikenros, C., Liberg, O., Wabakken, P., Flagstad, Ø., Milleret, C., Månsson, J., Svensson, L., Zimmermann, B., Åkesson, M., Sand, H., 2016. Estimating wolf (Canis lupus) population size from number of packs and an individual based model. Ecol. Modell. 339, 33–44. https://doi.org/10.1016/j.ecolmodel.2016.08.012

Ciucci, P., Reggioni, W., Maiorano, L., Boitani, L., 2009. Long-distance dispersal of a rescued wolf from the northern Apennines to the western Alps. J. Wildl. Manage. 73, 1300–1306. https://doi.org/10.2193/2008-510

Cubaynes, S., Macnulty, D.R., Stahler, D.R., Quimby, K.A., Smith, D.W., Coulson, T., 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). J. Anim. Ecol. 83, 1344–1356. https://doi.org/10.1111/1365-2656.12238

Donfrancesco, V., Ciucci, P., Salvatori, V., Benson, D., Andersen, L.W., Bassi, E., Blanco, J.C., Boitani, L., Caniglia, R., Canu, A., Capitani, C., Chapron, G., Czarnomska, S.D., Fabbri, E., Galaverni, M., Galov, A., Gimenez, O., Godinho, R., Greco, C., Hindrikson, M., Huber, D., Hulva, P., Jedrzejewski, W., Kusak, J., Linnell, J.D.C., Llaneza, L., López-Bao, J.V., Männil, P., Marucco, F., Mattioli, L., Milanesi, P., Milleret, C., Mysłajek, R.W., Ordiz, A., Palacios, V., Pedersen, H.C., Pertoldi, C., Pilot, M., Randi, E., Rodríguez, A., Saarma, U., Sand, H., Scandura, M., Stronen, A.V., Tsingarska, E., Mukherjee, N., 2019. Unravelling the scientific debate on how to address wolf-dog hybridization in Europe. Front. Ecol. Evol. 7, 175. https://doi.org/10.3389/fevo.2019.175

Fredrickson, R.J., Hedrick, P.W., 2006. Dynamics of hybridization and introgression in red wolves and coyotes. Conserv. Biol. 20, 1272–1283. https://doi.org/10.1111/j.1523-1739.2006.00401.x

Fritts, S.H., Mech, L.D., 1981. Dynamics, movements and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. 80, 79. https://doi.org/10.2307/3830611

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105, 1–41.

Gese, E.M., Mech, L.D., 1991. Dispersal of wolves (Canis lupus) in northeastern Minnesota, 1969- 1989. Can. J. Zool. 69, 2946–2955. https://doi.org/10.1139/z91-415

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Modell. 198, 115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: A review and first update. Ecol. Modell. 221, 2760–2768. https://doi.org/10.1016/j.ecolmodel.2010.08.019

Grosjean, P., 2018. Package "SciViews."

Haight, R.G., Mech, L.D., 1997. Computer simulation of vasectomy for wolf control. J. Wildl. Manage. 61, 1023–1031.

Haight, R.G., Travis, L.E., Nimerfro, K., Mech, L.D., 2002. Computer simulation of wolf-removal strategies for animal damage control. Wildl. Soc. Bull. 30, 844–852.

Harper, E.K., Paul, W.J., Mech, L.D., Weisberg, S., 2008. Effectiveness of lethal, directed wolf-depredation control in Minnesota. J. Wildl. Manage. 72, 778–784. https://doi.org/10.2193/2007-273

Hayes, R.D., Harestad, A.S., 2000. Demography of a recovering wolf population in the Yukon. Can. J. Zool. 78, 36–48. https://doi.org/10.1139/z99-186

Hedrick, P.W., Smith, D.W., Stahler, D.R., 2016. Negative-assortative mating for color in wolves. Evolution (N. Y). 70, 757–766.

Hindrikson, M., Remm, J., Pilot, M., Godinho, R., Stronen, A.V., Baltrūnaitė, L., Czarnomska, S.D., Leonard, J.A., Randi, E., Nowak, C., Åkesson, M., López-Bao, J.V., Álvares, F., Llaneza, L., Echegaray, J., Vilà, C., Ozolins, J., Rungis, D., Aspi, J., Paule, L., Skrbinšek, T., Saarma, U., 2017. Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management. Biol. Rev. 92, 1601–1629. https://doi.org/10.1111/brv.12298

Hradsky, B.A., Kelly, L.T., Robley, A., Wintle, B.A., 2019. FoxNet: An individual-based model framework to support management of an invasive predator, the red fox. J. Appl. Ecol. 56, 1460–1470. https://doi.org/10.1111/1365-2664.13374

Jedrzejewski, W., Branicki, W., Veit, C., Medugorac, I., Pilot, M., Bunevich, A.N., Jedrzejewska, B., Schmidt, K., Theuerkauf, J., Okarma, H., Gula, R., Szymura, L., Forster, M., 2005. Genetic diversity and relatedness within packs in an intensely hunted population of wolves Canis lupus. Acta Theriol. (Warsz). 50, 3–22. https://doi.org/10.1007/bf03192614

Jedrzejewski, W., Schmidt, K., Jedrzejewska, B., Theuerkauf, J., Kowalczyk, R., Zub, K., 2004. The process of a wolf pack splitting in Bialowieza Primeval Forest, Poland. Acta Theriol. (Warsz). 49, 275–280.

Jimenez, M.D., Bangs, E.E., Boyd, D.K., Smith, D.W., Becker, S.A., Ausband, D.E., Woodruff, S.P., Bradley, E.H., Holyan, J., Laudon, K., 2017. Wolf dispersal in the Rocky Mountains, Western United States: 1993–2008. J. Wildl. Manage. 81, 581–592. https://doi.org/10.1002/jwmg.21238

Kaczensky, P., 1999. Large carnivore depredation on livestock in Europe. Ursus 11, 59–72. https://doi.org/10.2307/3872986

Kramer-Schadt, S., Revilla, E., Wiegand, T., 2005. Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biol. Conserv. 125, 169–182. https://doi.org/10.1016/j.biocon.2005.02.015

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 (Cop.). 41, 647–660. https://doi.org/10.1111/ecog.02874

Lute, M.L., Carter, N.H., López-Bao, J. V., Linnell, J.D.C., 2018. Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. Biol. Conserv. 218, 223–232. https://doi.org/10.1016/j.biocon.2017.12.035

Mancinelli, S., Boitani, L., Ciucci, P., 2018. Determinants of home range size and space use patterns in a protected wolf (Canis lupus) population in the central apennines, Italy. Can. J. Zool. 96, 828–838. https://doi.org/10.1139/cjz-2017-0210

Marescot, L., Chapron, G., Chadès, I., Fackler, P.L., Duchamp, C., Marboutin, E., Gimenez, O., 2013. Complex decisions made simple: a primer on stochastic dynamic programming. Methods Ecol. Evol. 4, 872–884. https://doi.org/10.1111/2041-210X.12082

Marescot, L., Gimenez, O., Duchamp, C., Marboutin, E., Chapron, G., 2012. Reducing matrix population models with application to social animal species. Ecol. Modell. 232, 91–96. https://doi.org/10.1016/j.ecolmodel.2012.02.017

Marucco, F., McIntire, E.J.B., 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. J. Appl. Ecol. 47, 789–798. https://doi.org/10.1111/j.1365-2664.2010.01831.x

Marucco, F., Pletscher, D.H., Boitani, L., Schwartz, M.K., Pilgrim, K.L., Lebreton, J.-D., 2009. Wolf survival and population trend using non-invasive capture-recapture techniques in the Western Alps. J. Appl. Ecol. 46, 1003–1010. https://doi.org/10.1111/j.1365-2664.2009.01696.x

McManus, J.S., Dickman, A.J., Gaynor, D., Smuts, B.H., Macdonald, D.W., 2015. Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. Oryx 49, 687–695. https://doi.org/10.1017/S0030605313001610

Mech, L.D., 1987. Age, season, distance, direction and social aspects of wolf dispersal from a Minnesota pack, in: Mammalian Dispersal Patterns. University of Chicago Press, Chicago, IL, pp. 55–74.

Mech, L.D., Boitani, L., 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press.

Meier, T.J., Burch, J.W., Mech, L.D., Adams, L.G., 1995. Pack structure and genetic relatedness among wolf packs in a naturally-regulated population, in: Carbyn, L.N., Fritts, S.H., Seip, D.R. (Eds.), Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, Edmonton, AB, pp. 293–302.

Messier, F., 1985. Solitary living and extra-territorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. 63, 239–245.

Morrissey, M., 2018. Package “pedantics.”

Ovenden, T.S., Palmer, S.C.F., Travis, J.M.J., Healey, J.R., 2019. Improving reintroduction success in large carnivores through individual-based modelling: How to reintroduce Eurasian lynx (Lynx lynx) to Scotland. Biol. Conserv. 234, 140–153. https://doi.org/10.1016/j.biocon.2019.03.035

Packard, J.M., Mech, L.D., 1980. Population regulation in wolves, in: Biosocial Mechanisms of

Population Regulation. Yale University Press, New Haven, Connecticut, pp. 135–150.

Pilot, M., Greco, C., vonHoldt, B.M., Randi, E., Jędrzejewski, W., Sidorovich, V.E., Konopiński, M.K., Ostrander, E.A., Wayne, R.K., 2018. Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for the conservation status of hybrids. Evol. Appl. 11, 662–680. https://doi.org/10.1111/eva.12595

Pitt, W.C., Box, P.W., Knowlton, F.F., 2003. An individual-based model of canid populations: modelling territoriality and social structure. Ecol. Modell. 166, 109–121. https://doi.org/10.1016/S0304-3800(03)00130-3

R Core Team, 2014. R: A language and environment for statistical computing.

Railsback, S.F., Grimm, V., 2012. Agent-based and individual-based modeling: a practical introduction. Princeton University Press, Princeton, NJ.

Randi, E., 2011. Genetics and conservation of wolves Canis lupus in Europe. Mamm. Rev. 41, 99–111. https://doi.org/10.1111/j.1365-2907.2010.00176.x

Randi, E., Hulva, P., Fabbri, E., Galaverni, M., Galov, A., Kusak, J., Bigi, D., Bolfíková, B.Č., Smetanová, M., Caniglia, R., 2014. Multilocus detection of wolf x dog hybridization in Italy, and guidelines for marker selection. PLoS One 9, e86409. https://doi.org/10.1371/journal.pone.0086409

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science (80-.). 343, 1241484. https://doi.org/10.1126/science.1241484

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

Sidorovich, V.E., Stolyarov, V.P., Vorobei, N.N., Ivanova, N.V., Jedrzejewska, B., 2007. Litter size, sex ratio, and age structure of gray wolves, Canis lupus, in relation to population fluctuations in northern Belarus. Can. J. Zool. 85, 295–300. https://doi.org/10.1139/Z07-001

Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J.A., Boyd, D., Jimenez, M.D., Pletscher, D.H., Niemeyer, C.C., Meier, T.J., Stahler, D.R., Holyan, J., Asher, V.J., Murray, D.L., 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982–2004. J. Wildl. Manage. 74, 620–634. https://doi.org/10.2193/2008-584

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

Vonholdt, B.M., Stahler, D.R., Smith, D.W., Earl, D.A., Pollinger, J.P., Wayne, R.K., 2008. The genealogy and genetic viability of reintroduced Yellowstone grey wolves. Mol. Ecol. 17, 252–274. https://doi.org/10.1111/j.1365-294X.2007.03468.x

Wabakken, P., Sand, H., Liberg, O., Bjärvall, A., 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Can. J. Zool. 79, 710–725.

Wickham, H., RStudiom, R Core Team, 2019. Package “testthat.”

Appendix A

Complete description of the wolf individual-based model (IBM) following the Overview, Design concepts, and Details protocol ("ODD" protocol) developed by Grimm et al. (2006, 2010)

Overview

Purpose

The wolf IBM aims to represent all non-spatial dynamics that happen in a wolf population, with a focus to detail pack dynamics, the change of status between disperser and residents and the replacement of breeding individuals. Our model is different from the others (Marucco and McIntire 2010, Chapron et al. 2006; Pitt et al. 2003) on several aspects. First, we allowed adoption of young dispersing wolves by existing packs; the adoption is not a replacement of a missing breeder. Second, we specified an order for the breeder replacement with missing breeding females being replaced first by subordinates from their pack, and then by dispersers. It is the opposite for the replacement of the breeding male with missing breeder being first replaced by dispersers, then by one of the subordinates of the pack. Third, we included an avoidance of inbreeding in packs where mating between wolves more related than two cousins is prevented as much as possible. Fourth, we included a density-dependent mortality for resident adults when the population is at pack carrying capacity. Fifth, we allowed the movement of wolves in and out of the simulated population with possible immigrations and emigrations.

Entities, state variables, and scales

Entities in the model are wolf individuals. Each wolf has a unique ID, a sex (male or female), an age, a resident (i.e., belonging to a pack) or disperser status, a pack ID if it belongs to a pack, a breeding status if it is a breeding individual, a mother ID, a father ID, and a cohort ID. ID, sex,

mother ID, father ID and cohort ID never change during simulations. Age is updated each year. Resident or disperser status and pack ID change when an individual leaves or joins a pack. Breeding status changes when an individual become breeder, either by replacing a missing one or by forming its own pack. Packs are not considered as entities in the model as there is no mechanism acting on the whole pack at once. Packs are just a characteristic (via their ID) of the wolves. The model is non-spatial so the environment is not represented and wolves do not have a location associated. Temporal scale is a one-year time step.

Process overview and scheduling

In one year, all individuals go through the same series of sub-models (Fig. 1) and their state is modified according to the behavioral rules of each sub-model and their own characteristics. In order, these sub-models are: reproduction, aging, mortality, and change of status (Fig. 1). The change of the wolves' status is represented with several sub-models that, in order, are: pack dissolution, replacement of breeding females by subordinates, dispersal, migration, adoption, replacement of breeders by dispersers, establishment in pairs, establishment by budding, establishment alone, replacement of breeding males by subordinates (Fig. 1). Migration represents immigration of external wolves inside the simulated population and emigration of local wolves outside of the study area. This does not change the wolves' status *per se* but this sub-model needs to be included just after the dispersal (i.e., departures on wolves from their natal packs) (Fig. 1) to update the pool of dispersing individuals. (Fig. 1). In "reproduction", new individuals (pups) are produced. In "aging", the age of all individuals is updated. In "mortality", different mortality probabilities affect differently the individuals regarding their age, their resident or disperser status, and the number of existing packs regarding the pack carrying capacity. In "pack dissolution", some packs are dissolved regarding the age distribution in the pack, their number of individuals and number of breeders. If there are dissolution of some packs,

the resident status of the individuals is updated to dispersers and they lose their pack ID. In "replacement of breeding females by subordinates", female subordinates may replace the missing breeder in the pack so their breeding status is updated. In "dispersal", packs with too many individuals have some individuals leaving the pack with different probabilities regarding their age. These individuals have their resident status updated to dispersers and they lose their pack ID. In "immigration", wolves from outside integrate the population. In "emigration", wolves from the simulated population leave the study area; similar as if they die, they are removed from the population. In "adoption", young dispersing individuals may be adopted by small packs. These adoptees have their disperser status updated to resident and they obtain a pack ID. In "replacement of breeders by dispersers", dispersing individuals may replace missing breeders in packs. These individuals have their disperser status updated to resident, they obtain a pack ID and their breeding status is updated. In "establishment in pairs", two dispersing individuals of the opposite sex establish themselves together to form a new pack. These individuals have their disperser status updated to resident, they obtain a pack ID and their breeding status is updated. In "establishment by budding", a dispersing individual establish with a subordinate from a pack to form a new pack. The former disperser has it disperser status updated to resident, it obtains a pack ID and its breeding status is updated. The former subordinate obtains a new pack ID and has its breeding status updated. In "establishment alone", dispersers can establish themselves and form a pack alone. These individuals have their disperser status updated to resident, they obtain a pack ID and their breeding status is updated. In "replacement of breeding males by subordinates", male subordinates may replace the missing breeder in the pack so their breeding status is updated. At the end of this sub-models series, the information about the current population (i.e., the current characteristics of each individual) is saved and individuals go through again the same loop of sub-models, for as many years as simulated.

Design concepts

Basic principles

The life cycle of the wolf is represented through the reproduction, mortality, dispersal and establishment of the individuals, already defined in published wolf IBMs (Marucco and McIntire 2010, Chapron et al. 2016). However, extensive research in literature has been done to understand, and then include in the IBM, all processes regarding the change of status between residents and dispersers, the access to the breeding status, the pairing between male and female regarding their relatedness and the wolf status, the movement of wolves in and out of the population, and the density-dependent processes. The model provides new details on the pack dynamics to mimic the gray wolf life cycle as best as possible. The model is non-spatial but the distribution of the individuals is represented through their pack affiliation. The life cycle represented in the IBM as well as the parameter values used are more adapted to the wolf populations in central Europe (i.e., Alps) than for the North American populations.

Emergence

Through reproduction and immigration, new individuals are added in the population. Individuals die and are removed from the population through the different mortality and emigration processes. These changes in the population affect the total number of individuals. Processes affecting wolves depending on their individual characteristics (i.e., age, sex, resident or dispersing status, breeding status, etc.) affect the distribution of the individuals in different classes (e.g., number of residents and dispersers, number of packs with two breeders in it).

Adaptation

Wolves live in packs and most of the mechanisms coded in model depend on the pack structure and the status of the individuals in the pack. The presence of zero, one of two breeders constrains

the potential reproduction, pack dissolution, and replacement of breeding members. The total number of individuals in a pack constrains the pack dissolution, dispersal and adoption. The total number of established packs in the population also constrains some of the mechanisms as the different probabilities of establishment (i.e., in pairs, by budding and alone) and one mortality process are density dependent parameters.

Objectives

Wolves do not have an ultimate goal they need to fulfill over time. Individuals follow the behavioral rules of the different sub-models and respond to them according to their current characteristics and the current state of the packs.

Learning

There is no learning *per se* in the wolf IBM such as a learning of new skills (e.g., hunting preys taught by parents) but as individuals' age and status change, the possibilities for the individual change. For example, wolves of age 1, 2 and 3 years old can be adopted but not at an older age. Only mature wolves (of age 2 and older) can become breeder and establish a new territory; pups of 1 year old cannot. Only mature breeding wolves can reproduce; mature subordinates cannot.

Prediction

Individuals knows the current state of the population and individuals' current characteristics but they cannot predict any future population or individual state nor any individuals' actions.

Sensing

Wolves in packs have knowledge of all individual characteristics for the other members in their pack. Packs that can adopt young wolves can sense the presence of young dispersers. Dispersing individuals have access to the packs and their structure as replacement of missing breeders by dispersers and pairing with a subordinate from a pack is possible for these individuals. There is no sensing of the environment as there is no interaction with it.

Interaction

Wolves are social animals and therefore multiple interactions shape the life cycle of this species. Reproduction require two breeding individuals from the same pack to produce pups. Pack dissolution and dispersal represent a loss of interactions between individuals that were members of a pack and become dispersers due to various factors. In the replacement of the missing breeders, there is a choice among the mature subordinates of the pack or among the mature dispersers that may be constrained by the presence of the other breeding wolf to replace the missing one. During the establishment in pairs or by budding, a disperser interact with another disperser or a subordinate in a pack to create a new territory.

Stochasticity

Stochasticity is included in almost all components of the model. The number of pups produced per breeding pair, the number of individual dying, the maximum number of individual in a pack, the number of immigrants arriving in the population and the number of emigrants leaving are generated using probabilities. The following processes also happen following probabilities: the pack dissolution regarding the number of breeding members remaining in the pack, the adoption, the dispersal according to the individuals' age, and the establishment by budding. Also, a density-dependent probability constrains the different type of establishment (i.e., in pairs, by budding and alone) as well as adult mortality when the population is at pack carrying capacity. The sex of the pups, the choice between the non-related individuals to replace the missing breeders, the choice between the young dispersers to be adopted, the choice between the non-related individuals to partner with a disperser to establish, and the choice of the dispersing individuals that emigrate are done randomly with equal probabilities for every possibilities. In the immigration process, as nothing is known on the immigrant individuals, their sex and age (between a minimum and a maximum) is randomly chosen.

Collectives

Wolves belong to packs and their status of resident (i.e., inside a pack) or disperser (i.e., not belonging to a pack) affect almost all behavioral mechanisms they follow. However, there is no mechanism affecting the entire pack. As all individuals in the pack have different characteristics (i.e., age, sex, breeding status) they do not all respond in the same way.

Observation

The population is simulated for several years. Simulation outputs are available after each sub-model if needed or at the end of the whole series of sub-models at the end of the time step (i.e., at the end of the simulated year). The number of alive individuals with all their characteristics is available and many results can be extracted and derived from this population structure (e.g., the number of packs, the total abundance, the number of residents and dispersers, the number of breeders, the age distribution, etc.). We focused on results relevant for wolf conservation and management and defined 5 results. 1) The number of packs with two breeders. This metric is linked to the reproductive potential of the population and is of importance for management issues related to population growth. 2) The number of new packs formed in one year. This represents the pack turnover and the stability of the population that may affect hybridization and wolf-human conflicts. 3) The number of individuals with 4) the proportion of residents and dispersers in the population. Population size is often required in management control and knowing the distribution of the resident/dispersing status of the individuals may help understanding the population behavior. Finally, we looked at 5) the relatedness between the two breeders in each pack. Inbreeding avoidance plays a big part in the wolf life cycle, affecting the replacement of the missing breeders and the creation of new pack. Often under looked because hard to simulate in non-individual-based model, this factor may indicate missing pieces in the models when not well represented.

Details

Initialization

To launch the IBM, an initial wolf population is needed. We built a fictive population of 10 packs and 5 dispersing wolves, in a fictive environment that can hold 30 packs total (i.e., pack carrying capacity, Table 1). We created 5 packs with 2 breeders (one male and one female, 5 years old each) and 2 pups (one male and one female, 1 year old each); 3 packs with 2 breeders (one male and one female, 5 years old each), 1 yearling (one male, 2 years old) and 1 pup (one female, 1 year old); 2 packs with 2 breeders (one male and one female, 5 years old each) and 1 adult (one female, 3 years old); and 5 dispersers (3 females, 2 males, 2 years old each). This simple population was created for convenience but other initial populations can be defined by users. Table 1 list all parameters and their values used in the model. These parameters can also be modified by the user. However, they represent the best data available in literature for the gray wolf in Europe. Wolves do not have a precise location in this model as this IBM is non-spatial. The distribution of the individuals is represented through their pack affiliation.

Table 1: Parameters used in the wolf IBM.

Parameter	**Sub-model in which the parameter is used (see Fig. 1)**	**Explanation**	**Value**	**Reference**
Mean litter size	Reproduction	Number of pups that goes out of the female den. Mean	6.1	Sidorovich et al. 2007

		used for a Poisson distribution to generate the number of pups produced by a breeding pair.		
Pup mortality	Mortality	Mortality probability for wolves in their first year of their life.	0.602	Smith et al. 2010
Yearling mortality	Mortality	Mortality probability for non-dispersing yearlings.	0.18 (sd = 0.04)	Marucco et al. 2009
Non density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is not at pack carrying capacity.	0.18 (sd = 0.04)	Marucco et al. 2009
Density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is at pack carrying capacity. popDens is the population density per 1000 km2	1 - (1 / (1 + exp(-1.196 + (-0.505 * (popDens-53.833) / 17.984))))	Cubaynes et al. 2014
Pack carrying capacity	Mortality; Establishment in pairs; Establishment by	Maximum number of packs the environment within which the population is simulated can hold.	30	Defined by the user

	budding; Establishment alone			
Territory size	Mortality	Average territory size (in km^2) for wolves. Used to calculate the study area size with the pack carrying capacity to estimate wolf density through the model	104	Mancinelli et all. 2018
Dispersing pup mortality	Mortality	Yearly mortality probability for individuals that dispersed as pups and were not adopted by a pack during their dispersal year.	1	
Disperser mortality	Mortality	Yearly mortality probability for dispersers (except individuals that dispersed as pups).	0.31	Blanco and Cortes, 2007
Dissolution probability for pack with 1 breeder	Pack dissolution	Probability of dissolution for small packs that have only 1 breeding individual left in the pack.	0.258	Brainerd et al. 2008

Dissolution probability for pack with 0 breeder	Pack dissolution	Probability of dissolution for small packs that do not have any breeding individual left in the pack.	0.846	Brainerd et al. 2008
Pack size threshold for dissolution	Pack dissolution	Pack size to differentiate large (5.75 individuals) and small (2.36 individuals) packs. Packs with less individuals than this threshold are considered smalls and can dissolve if only 1 or 0 breeding member remains.	4.055	Brainerd et al. 2008
Relatedness threshold	Replacement of breeding females by subordinates; Establishment in pairs; Establishment by budding; Replacement of breeders by dispersers;	Relatedness value between 1st cousins. Two individuals must have their relatedness coefficient less or equal this threshold to mate.	0.125	Caniglia et al. 2014

	Replacement of breeding males by subordinates			
Mean pack size	Dispersal; Adoption	Mean number of individual in packs. Mean used for the Normal distribution to generate the maximum number of individuals in each pack.	4.405 (sd = 1.251)	Marucco and McIntire, 2010
Pup dispersal probability	Dispersal	Probability for a pup to leave the pack and become disperser when there are too many individuals in the pack.	0.25	Haight and Mech, 1997
Yearling dispersal probability	Dispersal	Probability for a yearling to leave the pack and become disperser when there are too many individuals in the pack.	0.5	Haight and Mech, 1997
Adult dispersal probability	Dispersal	Probability for an adult to leave the pack and become disperser when there are too	0.9	Haight and Mech, 1997

		many individuals in the pack.		
Number of immigrants	Immigration/ Emigration	Number of immigrants arriving in the population each year. All values have the same probabilities to be chosen.	0,1 or 2 (for our theoretical case studies)	Defined by the user
Proportion of emigrants	Immigration/ Emigration	Proportion of dispersing individuals that emigrate outside of the study area	0.1 (for our theoretical case studies)	Defined by the user
Probability of adopting	Adoption	Probability for a pack that has less member than its maximum pack size to adopt a young disperser.	0.5	
Probability of budding	Establishment by budding	Probability of success for a disperser to establish by budding. This probability is multiplied by the density-dependent probability of establishment for the dispersers.	0.5	

Input data

There is no input data in the model. The environment is not represented and the initial population is not built using data.

Sub-models

reproduction: Every packs with both a breeding male and a breeding female reproduce (Marucco and McIntire 2010). The number of pups each pair has is drawn in a Poisson distribution (Chapron et al. 2016) with a mean of 6.1 (Sidorovich et al. 2007), representing the number of pups that emerge from the female den. Each pup receives a unique ID. The sex of each pup is randomly chosen as male or female with a 1:1 ratio (Sidorovich et al. 2007, Marucco and McIntire 2010). Their age is set to 0 as all individuals (including these newborn pups) will go through the "aging" sub-model just after. Pups are considered as residents, with the pack ID of their parents. They are not breeders. Their mother and father IDs are recorded and they obtain the cohort ID related to the current simulated year (i.e., all pups born the same year have the same cohort ID).

aging: All individuals age of 1 year. Pups of the year are now 1 year old, yearlings are 2, and 3 years old and older are adults. Individuals are considered mature at 2 years old and older (i.e., yearling and adults).

mortality: There are 7 different mortalities, regarding the age, the dispersing status of the individuals and the total number of packs regarding pack carrying capacity. Mortality is applied individually to each wolf using a Bernoulli distribution. Pups have a probability of 0.602 to die (Smith et al. 2010). The mortality probability for non-dispersing yearlings is equal to 0.18 (sd = 0.04, Marucco et al. 2009). There are two types of mortality for non-dispersing adults that depends on the number of established packs in the population. If the number of established packs is below the pack carrying capacity of the area, mortality is fixed and similar to those of the

yearlings (i.e., equal to 0.18 (sd = 0.04, Marucco et al. 2009)). However, if the number of established packs is equal to the pack carrying capacity of the area, mortality is density-dependent. We used the equation linking wolf survival φ with wolf density from Cubaynes et al. (2014) to estimate the density-dependent mortality for non-dispersing adults: logit(φ) = 1.196 + (-0.505 * popDensStd), where popDensStd is the wolf density per 1000 km2 standardized with Cubaynes' mean and standard deviation values (mean = 53.833, sd = 17.984). Wolf density is calculated as the total number of wolves, without considering the pups, divided by the area where the population is, estimated as the pack carrying capacity defined by the user multiplied by the wolf average territory size (104 km2, Mancinelli et al. 2018). At that stage, no pup can be disperser and dispersing yearlings are individuals that dispersed the previous year (when they were pups due to a dissolution of their pack) but could not find a pack to adopt them during that year (otherwise they would be residents). We assumed pups are too young to survive by themselves and we defined a mortality probability equal to 1 to dispersing yearlings. All other dispersing wolves (i.e., adults) have a mortality probability equal to 0.31 (Blanco and Cortes 2007). We did not model senescence or any increase of the mortality probability with age. To represent realistic age distribution in the population, the limit for wolves was the end of their 15th year of simulation (Marucco and McIntire, 2010) and all individuals reaching 16 years old die.

packDissolution: Following the mortality event, packs of which social structure has been impacted by the loss of breeders may dissolve (Brainerd et al. 2008). Small packs with 1 breeding individual remaining will dissolve with a probability of 0.258 (Brainerd et al. 2008) and with a probability of 0.846 (Brainerd et al. 2008) when there is no breeder left. Packs are considered small when they have up to 4 individuals or less (i.e., mean between small and big packs; Brainerd et al. 2008). In the specific case where both breeders died and only pups remain, the pack always dissolves as we assumed pups alone are unlikely to maintain a territory and so they

disperse. When a pack dissolves, all former members of the pack become dispersers, they do not belong to a pack anymore and former breeding individuals lose their status.

replaceBreedingFemBySub: When a breeding female dies, she is most likely replaced by one of the female subordinates in her pack (most likely one of her daughters) (Caniglia et al. 2014; Jedrzejewski et al. 2005). When a pack is missing its breeding female, one of the mature females from the pack is randomly chosen to become breeder. Once the new breeding female is chosen we look at the relatedness between her and the current breeding male, if there is any. If there is a breeding male in the pack and he is too closely related to the chosen female, he may be replaced (in following sub-models *replaceBreederByDisp* and *replaceBreedingMalBySub*) by a disperser or a less related subordinate from the pack who will usurp the established breeding position (Mech and Boitani, 2003). The relatedness threshold chosen is the one of the first cousin (r = 0.125); a mating pair of breeding wolves can be cousins but no more related than this (e.g., no mating between siblings or parents and children) (Caniglia et al. 2014). This relatedness threshold is the same for all the following sub-models. This sub-model happens before the dispersal event to prevent subordinates that will potentially replace the breeding female to leave the pack.

dispersal: When a pack has too many wolves, some are chased away and become dispersers. A maximum number of individuals is generated for each pack at each time step using a Normal distribution with a mean of 4.405 (sd = 1.251, Marucco and McIntire 2010). If the pack has more wolves than its maximum threshold, some individuals will leave the pack until the number of wolves in the pack is equal to its threshold. Breeding individuals cannot disperse. All the other wolves can disperse but with different probabilities regarding their age. Pups may disperse with a probability of 0.25, yearlings have a probability to disperse equal to 0.5, and equal to 0.9 for the adults (Haight and Mech 1997). Wolves leaving the pack become dispersers and do not belong to the pack anymore.

immigration: Some wolves outside of the simulated population can arrive and interact with the other wolves. A determined number of immigrants will integrate the population. The sex of the immigrants is random (i.e., male or female with a 1:1 ratio). Their age is simulated using a truncated Poisson distribution of mean equal to 2 (with boundaries between 1 and 15) as yearlings are the most likely to disperse. Immigrants are dispersers, they do not belong to any pack yet and they are not breeder. As they were born outside the simulated population, they do not hold information about their mother ID, father ID or cohort ID. Immigrant wolves will react the same way (i.e., follow the same sub-model rules) as the native wolves.

emigration: A proportion of the current dispersing individuals, randomly chosen, leave the simulated population on a long-distance dispersal. These individuals will not come back and their disappearance is similar to simulating their death.

adoption: Packs which are not full (i.e., their number of individuals is below their maximum threshold) can adopt individuals with a probability of 0.5. These packs can adopt as many individuals until reaching their maximum number of pack members. Only the dispersers of 1, 2 and 3 years old can be adopted by these packs. The order of the packs adopting is random. Among potential adoptees, males are selected first. Then, if there are no more males and still places available for adoption, females are chosen. The choice among the males or among the females is random. Once young dispersers have been adopted, they become residents and belong to the pack that adopted them.

replaceBreederByDisp: Missing breeders in packs can be replaced by dispersers. First, we look at the packs missing breeding females. Mature female dispersers can become breeding females. If there is already a breeding male in the pack, we remove the dispersing females that are too closely related to the breeding male from the potential successors. Then, a female is randomly chosen among the unrelated ones to integrate the pack. All selected females become breeders of

their assigned pack, residents and belong to the pack they integrated. The order of the packs to fill the breeding female positions is random. After that, the same is done for the packs missing breeding males with mature male dispersers filling the positions, selected among genetically unrelated individuals that will mate with the breeding females of the packs if there are any. If there are packs where the missing breeding female was replaced by a subordinate (in *replaceBreedingFemBySub*) and the current breeding male was too related to her, the same is done for these packs with unrelated mature male dispersers usurping the established male breeders (Mech and Boitani, 2003). The breeding males replaced by dispersers are dismissed from their position and become subordinates in their own pack.

establishPairs: A male disperser and a female disperser can establish together and create a new pack. This is only possible if the number of existing packs is not already equal to the defined pack carrying capacity of the area. If the area is not already full, there is a density-dependent probability for dispersers to establish in pairs defined by a Bernoulli distribution with probability equal to the number of packs that can be created divided by the pack carrying capacity in packs of the area. The more packs, the less chance for the dispersers to establish themselves in pairs by creating a new pack. Only mature dispersers that are not too closely related can do so. Once a match is done between a male and a female disperser, they both become breeders, residents and obtain the same, new and unique pack ID related to the one they just created. The order for the choice of males and females among the available mature dispersers is random.

establishBudding: Budding is when a disperser and a mature subordinate wolf from an existing pack establish together to create a new pack. Similar to the establishment in pairs, it is possible only if the number of packs has not reached the pack carrying capacity. The probability for a disperser to bud is the density-dependence probability for establishment in pairs times a probability to bud equal to 0.5. This 0.5 factor makes budding less likely than forming a new

pack in pairs. Only mature dispersers can bud, and only with a non-breeding mature resident of the opposite sex that is not too closely related. Once there is a match between a disperser and a subordinate wolf to bud, they both become breeders, residents and obtain the same, new and unique pack ID to which they belong. The order for the choice of males and females among the available mature dispersers and subordinates in packs is random.

establishAlone: If the area is not at pack carrying capacity, remaining mature dispersers that could not establish themselves in pairs or by budding can establish themselves alone. The probability to establish themselves alone is also density-dependent (same as for the establishment in pairs). Once they establish by themselves, wolves become breeders, residents and obtain a new and unique pack ID to which they individually belong.

replaceBreedingMalBySub: When a breeding male is missing, it is most likely replaced by a disperser (Caniglia et al. 2014, Jedrzejewski et al. 2005, Vonholdt et al. 2008). However, if there was not any disperser to replace it, one of the subordinates in the pack can take over. When a pack is missing its breeding male, one of the mature male subordinates from the pack is chosen to become breeder. If there are several subordinates that can become successors, the choice is for the one the least related to the current breeding female, if there is one. If there are several subordinate males with the same least relatedness to the breeding female, or if there is not any breeding female, the choice is random. If the breeding female is too related to the newly chosen breeding male and there is a mature female subordinate less related, she will become breeding female and the current breeding female is dismissed (i.e., becomes subordinate). If there are several mature female subordinates least related, the choice among them is random. If the current breeding female is less or equally related to the breeding male than the mature female subordinates, she maintains her breeder status. In the particular case where there was a missing breeding female replaced by a subordinates (in *replaceBreedingFemBySub*) and the current

breeding male was too related to her, one of the male subordinates can take over the male breeding position, only if there is a male subordinate less related to the breeding female than him. If not, the breeding male keeps his position, mimicking the fact that wolves change partner to avoid incest, except when there is no better alternative (Mech and Boitani, 2003). Once new breeding individuals are chosen, they will be able to mate the next year.

Appendix B

Files: initParam.R, run.R and submodels.R

Files with R code to run the wolf IBM. The file initParam.R is to build the initial wolf population needed to launch the IBM simulations and to set the model parameters. The file submodels.R includes all sub-models used in the wolf IBM and detailed in the Methods. The file run.R runs the wolf IBM and extract some population results. It first call the submodel.R file to load all sub-models. Second, it calls the initParam.R file to create the initial population and load the model parameters. Then, a loop organizes the different sub-models, runs the simulation and records the outputs. Finally, some results are extracted from the saved model outputs and figures are produced. More comments are included in each file.

The files are available on the GitHub repository:
https://github.com/SarahBauduin/appendix_wolfIBM.
The model is under the GNU General Public License v3.0.

Appendix C

File: sensitivityAnalysisResults.xlsx

Complete results of the sensitivity analysis. The first line of the table is the name of the simulation runs: M0 for the original complete version of the model and the runs S1 to S42 are the runs similar as with M0 where one parameter of the model was modified, one at the time, with its value either decreased or increased by 5%. The second line informs which parameter was modified in the run and the following line gives the value used for this parameter. Then, the five following line are the five selected model outputs: the number of packs with a breeding pair, the number of new packs created, the number of individuals, the proportion of resident individuals and the relatedness between the individuals in breeding pairs. The result values are the mean values over the 200 simulation replicates for each run. The column "M0 [- 20%; + 20%]" presents the results for the run with M0 with the range - 20% and + 20% of the result values. Then, table cells are the mean values of the model outputs obtained with the runs S1 to S42. Dark orange cells are model results outside of the reference range of M0 results [- 20%; + 20%], light orange cells are the lowest and highest values for the model outputs.