BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2022), **97**, pp. 466–480.
doi: 10.1111/brv.12807

Patterns and determinants of dispersal in grey wolves (*Canis lupus*)

Ana Morales-González[1]*, Alberto Fernández-Gil[1], Mario Quevedo[2] and Eloy Revilla[1]

[1]*Department of Conservation Biology, Estación Biológica de Doñana (EBD-CSIC), Avd. Americo Vespucio 26, Sevilla, 41092, Spain*
[2]*Department of Organisms and Systems Biology, and Research Institute of Biodiversity (IMIB, UO-CSIC-PA), Oviedo University, Oviedo, Spain*

ABSTRACT

Dispersal is a key demographic process involving three stages: emigration, transience and settlement; each of which is influenced by individual, social and environmental determinants. An integrated understanding of species dispersal is essential for demographic modelling and conservation planning. Here, we review the dispersal patterns and determinants documented in the scientific literature for the grey wolf (*Canis lupus*) across its distribution range. We showed a surprisingly high variability within and among study areas on all dispersal parameters – dispersal rate, direction, distance, duration and success. We found that such large variability is due to multiple individual, social and environmental determinants, but also due to previously overlooked methodological research issues. We revealed a potential non-linear relationship between dispersal rate and population density, with dispersal rate higher at both ends of the gradient of population density. We found that human-caused mortality reduces distance, duration and success of dispersal events. Furthermore, dispersers avoid interaction with humans, and highly exposed areas like agricultural lands hamper population connectivity in many cases. We identified numerous methodological research problems that make it difficult to obtain robust estimates of dispersal parameters and robust inferences on dispersal patterns and their determinants. In particular, analyses where confounding factors were not accounted for led to substantial knowledge gaps on all aspects of dispersal in an otherwise much-studied species. Our understanding of wolf biology and management would significantly benefit if wolf dispersal studies reported the results and possible factors affecting wolf dispersal more transparently.

Key words: emigration, transience, settlement, dispersal rate, dispersal distance, dispersal success, density-dependence, human-caused mortality

CONTENTS

* Address for correspondence (Tel: +34 639 488171; E-mail: moralesglezana@gmail.com)

I. INTRODUCTION

Dispersal plays a central role in the dynamics and persistence of spatially structured populations (Bowler & Benton, 2005; Revilla & Wiegand, 2008; Clobert *et al.*, 2009). Among other effects, it allows gene flow between populations, can rescue small local populations from extinction, and enables the colonization of available habitat (Ronce, 2007). A good understanding of species dispersal is paramount to predict population dynamics accurately and to help in decision making for management and conservation.

The dispersal process consists of three stages connected by behavioural decisions: emigration from the natal territory, transience through unfamiliar areas, and settlement in a new area (Clobert *et al.*, 2009). Individual strategies at each dispersal stage vary due to multiple determinants (Bowler & Benton, 2005; Ronce, 2007; Nathan *et al.*, 2008; Clobert *et al.*, 2009; Matthysen, 2012; Morales-González *et al.*, 2019), which can be grouped into: the internal state of dispersers, e.g. age, sex and body size; and external determinants, including social – e.g. conspecific and heterospecific density – and environmental factors – e.g. prey availability and human-caused mortality.

The influence of individual, social and environmental determinants on dispersal vary among species as do their life histories (Bowler & Benton, 2005). In group-living species, cooperation among group members entails a high degree of complexity. Offspring receive a variety of benefits by remaining in the natal group, such as reduced dispersal mortality, access to breeding opportunities in the natal group, increased foraging efficiency and defence, or indirect fitness benefits due to alloparental care (Ekman, Sklepkovych & Tegelstrom, 1994; Clutton-Brock, 2002; Sparkman *et al.*, 2011). However, remaining in the natal group also carries costs: kin competition, higher risk of inbreeding, energy expenditure in helping behaviour and delayed reproduction (Heinsohn & Legge, 1999). The balance between the costs and benefits of cooperation will govern whether an individual disperses or remains in the group, with this trade-off varying in time, space and between individuals. For instance, low population densities may reduce the benefits of cooperation potentially triggering dispersal, whilst high population densities may increase kin competition either prompting dispersal or delaying it (Revilla & Palomares, 2002; Maag *et al.*, 2018).

The grey wolf *Canis lupus* is a social canid species structured in family groups known as packs averaging from three to eleven individuals (Fuller, Mech & Cochrane, 2003; Fernández-Gil *et al.*, 2020). Packs generally consist of a dominant pair that monopolizes reproduction (the basic social unit) and their offspring, which often disperse at sexual maturity to form new packs. Dispersers can also join existing packs and may engage in secondary dispersal events between consecutive packs (Mech & Boitani, 2003).

Historically, wolves occupied large continuous areas throughout the northern hemisphere, but during the 19th and 20th centuries they were extirpated from much of their former range, remaining in areas with low human impact (Paquet & Carbyn, 2003). In recent decades, some wolf populations in North America and Europe are recovering due to changes in land cover and human population density patterns among others factors (Chapron *et al.*, 2014; Ripple *et al.*, 2014; Cimatti *et al.*, 2021). However, as wolf populations recover and expand, lethal management (i.e. culling, hunting and/or trapping) has been demanded by some stakeholders, and implemented in many areas as a controversial management tool (Musiani & Paquet, 2004; Fernández-Gil *et al.*, 2016). In addition, illegal wolf killing commonly occurs (Liberg *et al.*, 2012; Treves *et al.*, 2017). Direct and indirect human-induced mortality can potentially affect dispersal with profound consequences on population dynamics (Quevedo *et al.*, 2019; Recio *et al.*, 2020).

The study of wolf movements was greatly facilitated by the use of radio-tracking, concurrent with the start of the recovery of wolf populations (Mech, 1967). Since then, much information about wolf dispersal has emerged (Mech & Frenzel, 1971; Gese & Mech, 1991; Boyd *et al.*, 1995; Kojola *et al.*, 2006; Jimenez *et al.*, 2017). Additionally, global positioning system (GPS) tracking technology and advanced genetic approaches have been used in recent years (Horne *et al.*, 2019; Barry *et al.*, 2020; Bassing *et al.*, 2020). However, existing dispersal data are mostly scattered and disconnected across the literature, providing a complex picture of dispersal patterns and causations. Recently, Mech (2020) discussed potential determinants of two types of movement patterns during natal dispersal: long-distance dispersal and coincidental dispersal. Nevertheless, there is paucity of studies integrating the available information to show where it converges and to provide a better understanding of the mechanisms behind the dispersal process. The applicability of a more integrated understanding ranges from projecting the dynamics of wolf populations under different natural and human conditions, including shifts in distribution ranges and connectivity between subpopulations, to locating areas with high livestock depredation risk (Marucco & McIntire, 2010).

Herein, we provide a synthesis of the existing literature on grey wolf dispersal with the following objectives: (*i*) to identify the existing variability within and among study areas for dispersal parameters related to the three stages of grey wolf dispersal: dispersal rate, direction, distance and duration, and success; (*ii*) to identify dispersal patterns and their determinants; and (*iii*) to identify methodological research issues, knowledge gaps and current research needs.

II. METHODS

We conducted a systematic review of the literature on grey wolf dispersal across its distribution range. We located studies by using Elsevier's *Scopus* database and multiple terms that represent different parameters of grey wolf demography, including dispersal: ('grey wolf' OR '*Canis lupus*') AND ('demography' OR 'demographic' OR 'population' OR 'density' OR 'abundance' OR 'survival' OR 'survive' OR 'mortality' OR 'die' OR 'reproduction' OR 'reproductive'

OR 'reproduce' OR 'movement' OR 'move' OR 'dispersal' OR 'emigration' OR 'immigration' OR 'solitary' OR 'lone' OR 'mating' OR 'pregnancy' OR 'birth' OR 'denning' OR 'breeding' OR 'rendezvous' OR 'maturity' OR 'recruitment' OR 'home range' OR 'core area' OR 'litter size' OR 'pack size' OR 'collar' OR 'telemetry'). A first search was done for the title, key words and abstract of articles in English published before 2020. We sorted the search results by relevance (i.e. articles that most closely matched the searched words) and reviewed the first most-relevant 250 studies. The same search was performed for the period January 2020 to September 2021 and all the resulting articles were reviewed. We also searched the references provided in the literature sections of all retrieved articles.

The publications with dispersal information ($N = 69$) were retained, categorized and examined according to the three stages of dispersal and related dispersal parameters: (*i*) emigration phase – dispersal rate ($N = 34$ papers); (*ii*) transience phase – dispersal direction ($N = 22$) and dispersal distance and duration ($N = 45$); and (*iii*) settlement phase – dispersal success ($N = 34$). Publications that addressed several topics were included in more than one category. We retrieved the numerical/categorical data on dispersal parameters and provide the information as online Supporting Information: (*i*) dispersal rates (Table S1); (*ii*) dispersal distance and duration (Table S2); and (*iii*) dispersal success (Table S3). Data were based on ear-tagged, radio-collared and/or genotyped wolves. We also retrieved information on the individual, social and environmental (including natural and human) determinants of dispersal and documented dispersal patterns. Below we present a descriptive summary and a critical appraisal of all collected information. We plotted the spatial location of each reviewed study (except for seven review articles with no specific spatial location) on a worldwide map using ArcGIS 10.3 software (ESRI, 2014), to which we added the species distribution map according to the IUCN *Red List of Threatened Species* (Boitani, Phillips & Jhala, 2018) (see Fig. S1). Note that there is more information available from the USA and western Eurasia than for remaining range of this species.

We defined wolf dispersal as it has been commonly defined in the literature: the permanent movement of an individual wolf from the territory of the pack in which it was a member (referred to as 'initial territory') to a territory where the individual established for potential reproduction. The definition included natal dispersal events – i.e. the initial territory corresponded to the natal one; and secondary or breeding dispersal events – i.e. the initial territory was not the natal one. Regarding the dispersal stages, emigration referred to the moment at which individuals left the initial territory. Emigration marked the beginning of transience, where individuals moved away from the initial territory. We considered settlement to occur when the disperser: (*i*) formed a new pack, i.e. established a new territory with at least one other wolf of the opposite sex; or (*ii*) joined an existing pack. In the former case, pairing may have occurred at a different time: the disperser first paired and then both found a suitable territory to settle or the disperser first found and remained in a suitable territory (i.e. established in a territory) where it finally paired and therefore settled. Finally, we considered reproduction after settlement as the ultimate objective of dispersers. We considered different measurements of dispersal success: at establishing in a territory (a new or an existing one), at pairing (before or after establishment), at denning (i.e. whether denning occurred) and at reproducing (i.e. offspring confirmed at 3 weeks of age or later). A summary description of key concepts used throughout this review is provided in Table 1.

III. RESULTS

(1) Emigration stage – dispersal rates

We extracted numerical data on dispersal rates from 24 out of 34 articles (Table S1). We distinguished between three types of dispersal rates: (*i*) the proportion of wolves monitored that dispersed during the study period; (*ii*) the estimate of the proportion of wolves in the population that dispersed per year (i.e. annual dispersal rate); and (*iii*) the estimate of the proportion of wolves in the population that dispersed per month (i.e. monthly dispersal rate). Annual dispersal rate varied among study areas (Fig. 1). However, comparisons should be made with caution since the methodologies used to obtain these dispersal rate estimates varied widely. This variation included the treatment given to wolves with unknown fate – i.e. assuming they died or dispersed or excluding them from analysis – and the statistical approach used – i.e. based on the number of monitored wolves, the period of time that each wolf was monitored, or other complex functions. It is necessary to define an appropriate methodology to be used consistently in future research. Annual dispersal rate varied among years within the same study area (Fig. 1), with a maximum recorded rate of 0.79. In addition to methodological differences, the individual, social and environmental determinants discussed below (summarized in Table 2) will contribute to explain the variability observed in dispersal rates among and within study areas.

A review of North American studies revealed similar dispersal rates for yearlings (i.e. 12–23 months) and adults (i.e. ≥24 months) when breeding wolves, which rarely dispersed, were removed from the analysis (Fuller, Mech & Cochrane, 2003). No or rare dispersal was reported for pups (i.e. <12 months) (Fritts & Mech, 1981; Peterson, Woolington & Bailey, 1984; Messier, 1985; Ballard, Whitman & Gardner, 1987; Jimenez *et al.*, 2017). The youngest and oldest dispersers documented were 8 months (Mech *et al.*, 1998) and 7.5 years old (Boyd *et al.*, 1995), respectively. Although most studies found males and females to disperse at similar rates (Peterson, Woolington & Bailey, 1984; Fuller, 1989; Gese & Mech, 1991; Boyd *et al.*, 1995; Ballard *et al.*, 1997; Pletscher *et al.*, 1997; Boyd & Pletscher, 1999; Kojola *et al.*, 2006; Blanco & Cortés, 2007), a study based on a large

Table 1. Summary description of key concepts used throughout this review on grey wolf dispersal

Concept	Description
Dispersal	The permanent movement of an individual wolf from the territory of the pack in which it was a member to the territory where the individual established for potential reproduction.
Stages	Emigration from the natal territory, transience through unfamiliar areas, and settlement in a new area.
Strategies	Decisions made at each dispersal stage, e.g. direction taken during transience.
Parameters	Variables stemming from individual strategies at each dispersal stage, i.e. dispersal rate, direction, distance, duration and success.
Patterns	Predominant individual strategies in the set of wolves studied.
Determinants	Factors that influence individual strategies at each dispersal stage and that we grouped as individual, social, and environmental (i.e. natural and human).
Rate	Calculated as: the proportion of wolves monitored that dispersed during the study period; the estimate of the proportion of wolves in the population that dispersed per year (i.e. annual dispersal rate); and the estimate of the proportion of wolves in the population that dispersed per month (i.e. monthly dispersal rate).
Direction	The travelling routes selected by wolves during transience and the destination areas to which they head.
Distance	Kilometres from the disperser's initial pack territory/capture location (the latter for individuals already dispersing when monitoring started and whose initial territory was unknown) to the territory where the disperser established for potential reproduction, the mortality location or the last known location of the individual while dispersing.
Duration	Time period from emigration from the disperser's initial pack territory/capture location (the latter for individuals already dispersing when monitoring started) to the establishment in a territory for potential reproduction, the mortality or the last known location of the individual while dispersing.
Success	Measured as success at establishing in a territory (a new or an existing one), success at pairing (before or after establishment), success at denning (i.e. whether denning occurred), and success at reproducing (i.e. offspring confirmed at 3 weeks of age or later).

data set (Jimenez *et al.*, 2017) showed a male-biased dispersal rate. The latter may reflect a difference in life-history strategies between the sexes, such as a higher likelihood of subordinate females attaining breeding position in their natal pack (Jędrzejewski *et al.*, 2005; Vonholdt *et al.*, 2008; Caniglia *et al.*, 2014). In spite of the discussed effects, Jimenez *et al.* (2017) found that individual features were not powerful predictors of annual dispersal rates.

Population density (for both individuals and packs) may be an important predictor of dispersal rates within populations according to the following results (but see Hayes & Harestad, 2000): (*i*) areas recently colonized by wolves generally showed high dispersal rates of yearlings (Fritts & Mech, 1981; Boyd *et al.*, 1995; Kojola *et al.*, 2006); (*ii*) overall dispersal rate in a colonizing population declined an estimated 4% for every unit increase in packs/1000 km^2, with pack density being a good predictor of annual dispersal rates (Jimenez *et al.*, 2017); and (*iii*) Gese & Mech (1991) reported an increase in the dispersal rate of pups and yearlings when the density of wolves reached the maximum predicted according to prey availability. These results further suggest a non-linear relationship between dispersal rate and population density within populations: dispersal rate is greatest at lower and higher densities and lowest at medium densities. A similar non-linear relationship has been observed in other species (e.g. *Suricata suricatta*; Maag *et al.*, 2018) and is consistent with theoretical predictions. At lower population densities limited benefits provided by cooperation can enhance dispersal in social species (Hoogland, 2013). In addition, at low population densities the higher availability of vacant areas in which to establish new packs may promote dispersal, with wolves likely obtaining such information through extra-territorial travel. At moderate densities, the benefits of cooperation are expected to increase and exceed the costs of kin competition, thus making individuals more likely to remain in the group (Clutton-Brock, 2002), and the reduced availability of vacant areas also may favour remaining in the group. At higher population densities (generally also involving large group sizes), the costs of kin competition are expected to increase and exceed the benefits of cooperation, thus prompting dispersal (Cote, Clobert & Fitze, 2007). The decline in dispersal rate from low to medium population density supports the prediction that population density favours the evolution of delayed dispersal and philopatry in cooperative breeders (Kokko & Lundberg, 2001).

Dispersal may be more likely in large packs. The mean size of packs from which wolves dispersed in the Rocky Mountains was larger than the mean overall pack size (Jimenez *et al.*, 2017). Nevertheless, mean pack size was not a significant predictor of annual population dispersal rates (Jimenez *et al.*, 2017). Most dispersals are documented during late autumn, winter and spring (Fritts & Mech, 1981; Peterson, Woolington & Bailey, 1984; Ballard, Whitman & Gardner, 1987; Mech, 1987; Fuller, 1989; Gese & Mech, 1991; Boyd *et al.*, 1995; Boyd & Pletscher, 1999; Kojola *et al.*, 2006; Adams *et al.*, 2008; Jimenez *et al.*, 2017). Several studies speculated that social interactions within packs occurring during these periods act as ultimate determinants: food shortage for yearlings resulting from large pups still being provisioned with food during late autumn (Mech *et al.*, 1998; Mech &

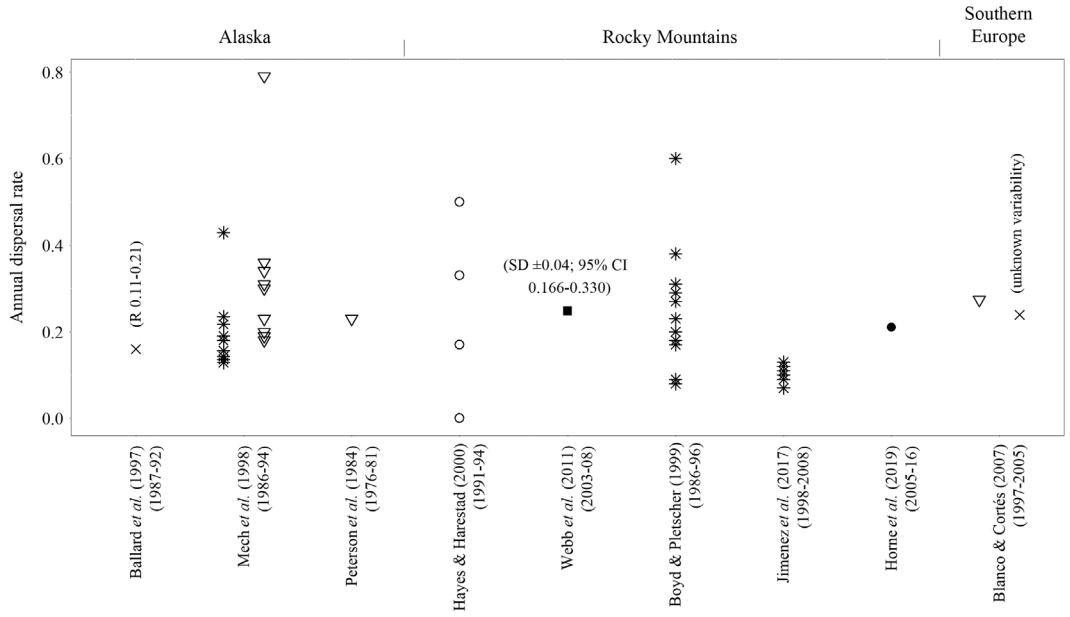

Fig 1. Annual dispersal rates documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range. The study periods are provided below each reference on the *x*-axis. Variability corresponding to mean values is shown in brackets: R, range; SD, standard deviation; 95% CI, 95% confidence interval. Different symbols indicate different methods used to obtain dispersal rates: asterisk = the number of dispersal events detected in a given year was divided by the number of wolves monitored in that year; white triangle = the number of dispersal events detected in a given year/during the study period was divided by the number of wolf-years of monitoring in that year/during that study period for Mech *et al.* (1998) and Blanco & Cortés (2007), respectively, or the number of dispersal events detected in a given month was divided by the number of wolf-months of monitoring in that month (months pooled across years) for Peterson, Woolington & Bailey (1984); cross = used the approach of Heisey & Fuller (1985) to estimate survival; black rectangle = used a non-parametric cumulative incidence function estimator developed by Heisey & Patterson (2006); black circle = the probability of pack members transitioning to dispersal state each month was modelled using the known fates of GPS-collared wolves; white circle = method used to estimate the dispersal rate not specified in the original study. Monthly dispersal rates were transformed into annual rates. Detailed description of the methods and dispersal rates per age class are available in Table S1.

Boitani, 2003); increased aggression by breeding wolves over subordinates during the mating period (i.e. winter) (Zimen, 1976); or increased levels of social interactions between parents and pups and social distancing with other pack members during the early pup-rearing period (i.e. spring) (Boyd & Pletscher, 1999). One study found that changes in dispersal rate across seasons applied only to young individuals, while adults older than 2 years dispersed at a similarly low rate throughout the year (Adams *et al.*, 2008). Finally, breeder turnover in an established population did not affect the number of helpers aged ≥2 years present in groups (Ausband, Mitchell & Waits, 2017), suggesting that subordinates do not exhibit increased dispersal after breeder turnover. However, the loss of breeders in small packs, in contrast to large packs, can result in pack dissolution and dispersal of all pack members, with a higher dispersal probability if no breeders are left (Brainerd *et al.*, 2008).

Dispersal rate, mainly that of yearlings (Mech *et al.*, 1998; Fuller, Mech & Cochrane, 2003), increases when per capita prey availability is scarce (Messier, 1985; Peterson & Page, 1988; Gese & Mech, 1991; Hayes & Harestad, 2000). The minimum daily energetic requirement for a wild wolf is 0.09 kg per kg of wolf per day (Peterson & Ciucci, 2003). Without access to sufficient prey, competition and social stress within packs may force young wolves to disperse (Zimen, 1976). Another environmental determinant that may influence dispersal are epidemic outbreaks. For example, dispersal rate increased in Alaska following a rabies epizootic, perhaps due to the disruption of pack social structure following mortalities.

Results from some studies suggest that human-caused mortality reduces population dispersal rates in established populations (but see Horne *et al.*, 2019). Webb, Allen & Merrill (2011) reported low dispersal rates in a population with high human-induced mortality, and Jimenez *et al.* (2017) found higher dispersal rates and different seasonal patterns of dispersal rates in relatively undeveloped lands with low human-caused mortality than in lands highly modified by humans where human-caused mortality occurred at moderate to high rates. As argued by these authors, human-caused mortality in established populations may reduce dispersal of individuals through decreased resource competition due to direct losses of individuals, mostly youngsters with a higher likelihood of dispersing. However, it is possible that the

Table 2. Summary of the effects of individual, social and environmental determinants of dispersal documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range

			Dispersal stages			
			(1) Emigration	(2) Transience		(3) Settlement
Determinants			Rate	Direction[a]	Distance & duration	Success[b]
Individual	Age		Yearlings = adults; low for pups		−	+
	Social status		Breeding wolves < subordinates			
	Sex		Male ≥ female		Male ≥ female	Female > male
	Genetics			Genetically determined*		Decreases for inbred wolves
Social	Population density		Low > medium < high*	Territories in higher density areas*	Unclear*	−
	Pack size		+			– Immigrant acceptance*
	Social interactions within the pack		Increases during mating, early pup rearing and late autumn travels			
	Breeder turnover		No effect*			
	Death of breeder/s		Increases for small packs			Trigger immigrant acceptance
	Presence of pack territories			Avoidance *versus* frequent visits*		
	Density of competitors			Territories in lower density areas		
	Availability of unrelated mates				–*	
	Creating *versus* joining pack					Creating > joining pack
Environmental	Natural	Per capita prey availability	−	Unclear*		
		Epidemic outbreaks	Increases*			
		Landscape features		Habitat corridors*; territories in forested and mountainous areas[c]		
	Human	Human-caused mortality	–*	Ecological trap*	–*	–*
		Habitat modification	No effect*		–*	
		Landscape features		Avoidance[c]		

The effects of the different determinants are shown for the three stages of dispersal: (1) emigration – dispersal rate; (2) transience – dispersal direction, distance and duration; and (3) settlement – dispersal success. Positive (+) and negative (−) effects are indicated. Asterisks indicate where further research is especially needed. Blank cells indicate no information available.
[a]The characteristics of the natal habitat influence dispersal direction. Dispersing wolves select natal-like habitats for territory establishment.
[b]Dispersal distance, a behavioural decision taken during transience, reduces dispersal success.
[c]Dispersers avoid interactions with humans. Researchers use natural and anthropogenic landscape features as proxies of human activity levels and risk of exposure to humans.

expected increase in poaching when applying lethal management to wolf populations (Chapron & Treves, 2016; Santiago-Ávila, Chappell & Treves, 2020) could lead to underestimates of dispersal rates, because poached wolves will often remain undetected (Treves *et al.*, 2017).

A widespread belief is that wolf populations can compensate for human exploitation rates of ≤0.29 wolves per year. This arose from the observation that exponential growth rates reported from North American wolf studies were generally positive or stable below annual human-caused mortality rates of 0.29 wolves [see Adams *et al.*, 2008 for an update of Fuller, Mech & Cochrane, 2003]. Adams *et al.* (2008) concluded that compensation occurred *via* adjustments in dispersal components (i.e. reduced dispersal rates and emigration from populations and increased immigration). However, neither dispersal nor

other factors that could influence growth rates (e.g. pup production) were quantified. More importantly, the growth rate data were from local sites within populations, meaning that they did not account for wolves adjacent to these studied local sites which were also part of the population, and making inferences of the dynamics of entire populations potentially misleading. In an update of previous analyses, Creel & Rotella (2010) found that growth rates declined across all observed levels of human-caused mortality, including low levels.

Finally, whether the degree of habitat modification by humans affects dispersal rates remains to be investigated, although some authors (Blanco & Cortés, 2007) observed apparently similar dispersal rates in Spanish agricultural areas with dense networks of roads and in several locations in North America with different degrees of habitat modification, suggesting a lack of effect.

(2) Transience stage

(*a*) *Dispersal direction*

According to the literature, individual, social and environmental factors all influence wolf dispersal direction, i.e. the travelling routes selected by wolves during transience and the destination areas to which they head.

Dispersing wolves select habitats similar to their natal site for territory establishment when dispersing short distances (Sanz-Pérez *et al.*, 2018) in a process known as natal habitat preference induction (see Davis & Stamps, 2004). This process seems the most probable explanation for the observed correlation of the spatial genetic structure across wolf ranges with climate, habitat type and wolf diet composition (see Geffen, Anderson & Wayne, 2004; Pilot *et al.*, 2006; Leonard, 2014). Natal habitat preference induction may also explain cases of coincidental dispersal by wolves (Mech, 1987; Boyd & Pletscher, 1999; Kojola *et al.*, 2006; Gable *et al.*, 2019) from a given area in the same directions and over the same distances. There could also be habitat corridors facilitating similar dispersal routes as seen for other species (Berggren, Birath & Kindvall, 2002). However, a recent review on coincidental dispersal (Mech, 2020), hypothesized that dispersal direction may be, at least to some degree, genetically predisposed, similar to dispersal distance in bird species (Pasinelli, Schiegg & Walters, 2004).

Sanz-Pérez *et al.* (2018) found that dispersing wolves established their territories in the areas with the highest wolf densities, and some studies (Wydeven, Schultz & Thiel, 1995; Boyd & Pletscher, 1999) reported frequent dispersal from colonizing populations to source populations. These results do not necessarily indicate that a high fraction of these individuals are simply using the presence of conspecifics as a cue; other cues of patch quality may be attracting them to those areas (see Doligez *et al.*, 2003). Among other cues used for dispersal is the density of interspecific competitors such as brown bears *Ursus arctos*, which negatively affects territory establishment (Sanz-Pérez *et al.*, 2018).

Sanz-Pérez *et al.* (2018) found that density of the main prey did not influence territory establishment. This is not surprising if secondary productivity was not limiting. However, the existing high levels of human-caused mortality in the studied population may also have influenced their results. For instance, individuals may have selected habitats rich in prey but they may not have succeeded at establishing a territory if human-caused mortality levels were too high. Indeed, some studies observed dispersal to areas with moderate to high human-caused mortality that harboured abundant food resources and potential vacant habitats (Potvin, 1988; Kojola *et al.*, 2006). Conceivably, human-caused mortality creates ecological traps as noted for other species (Delibes, Ferreras & Gaona, 2001; Schlaepfer, Runge & Sherman, 2002; Morales-González *et al.*, 2020). Additional research is required to shed light on the role of human-caused mortality and the use of food availability as a cue for territory establishment.

The majority of the studies indicate that dispersal direction is strongly influenced by the risk of interaction with humans. Researchers use natural and anthropogenic landscape features as proxies of human activity levels and risk of exposure to humans. Although highly context dependent (see Sazatornil *et al.*, 2016), wolves tend to establish territories in forested and mountainous areas with less human infrastructure such as buildings and roads (Boyd *et al.*, 1995; Sanz-Pérez *et al.*, 2018; Barry *et al.*, 2020). Wolves strongly avoid human infrastructure, in particular houses and primary roads and to a lesser extent forest roads, across all life stages (Barry *et al.*, 2020). However, Barry *et al.* (2020) also found an increase in wolf use of human infrastructures during dispersal compared to the natal stage, even after controlling for changes in availability. Improved mobility through the landscape and hunting efficiency have been proposed to motivate road use (Barry *et al.*, 2020; Dickie *et al.*, 2020). Wolves move faster while on human linear features (Dickie *et al.*, 2020) and during dispersal (Barry *et al.*, 2020) but this may simply be a response to lower landscape quality and higher risk of mortality during dispersal. Main motorways, urban centres and agricultural areas reduce population connectivity in many areas by acting as important barriers to wolf dispersal (Jędrzejewski *et al.*, 2004; Rodríguez-Freire & Crecente-Maseda, 2008; Dondina *et al.*, 2020), and individual variation likely results in some wolves dispersing through multi-use habitat and crossing what might be considered impediments to colonize new regions (Mech, Fritts & Wagner, 1995; Linnell *et al.*, 2005; Ciucci *et al.*, 2009).

Results from several studies suggest that presence of pack territories influences travelling routes selected by wolves: while some studies found locations of dispersers almost exclusively in areas not utilized by packs or along the periphery of pack territories (Fritts & Mech, 1981), others documented that dispersers frequently visited pack territories (Messier, 1985; Boyd *et al.*, 1995; Blanco & Cortés, 2007). In areas where habitat is limiting (e.g. Messier, 1985), dispersers may be forced to travel through pack territories. However, differences in movement patterns with

respect to pack territories also occurred between increasing populations with abundant food supply (Fritts & Mech, 1981; Boyd *et al.*, 1995) and causes of such differences remain unknown.

(*b*) *Dispersal distance and duration*

We extracted numerical data on dispersal distance and duration from 36 out of 45 articles (Table S2). We identified two types of limitations on the data. (*i*) Problems associated with the difficulty of monitoring the dispersal process in an elusive carnivore. In many cases, monitoring of dispersal events was incomplete, e.g. monitoring started with the individual already dispersing and/or ended before the individual finally established in a territory for future reproduction or died while dispersing (Table S2). Such issues mean that comparisons must be made with care to avoid bias. Moreover, it must be highlighted that published dispersal data are already biased towards short-distance movements and thus must be considered as conservative minima. This is because data on dispersal are often obtained during investigations focused on resident wolves, and when dispersers move beyond the limits of the study area their monitoring becomes difficult and they are often no longer followed. Such 'lost' dispersals are only detected if animals are killed and reported by chance. Recent technological progress in animal tracking has contributed enormously to the systematic collection of dispersal data. (*ii*) We identified limitations associated with the resolution of the data shared by researchers. Some studies did not clearly specify the sites and periods over which each dispersal event was monitored (Table S2). This adds uncertainty to the results and can prevent other researchers from using these data in future research.

We distinguished between three types of measurements of distance of dispersal events: straight-line distances; minimum distances, i.e. sum of straight-line distances between successive relocations of dispersers; and actual distances. The straight-line distance travelled by wolves varied among and within study areas (Fig. 2A), ranging from *ca.* 0 km (i.e. bordering territories) to 1092 km. The minimum distance covered by dispersers varied from 41.2 km (relocation frequency = 8 locations per day) to 3950 km (relocation frequency = 6 locations per day) (Fig. 2B). Note that the frequency of relocations is a critical factor; the higher the frequency, the more accurate will the minimum distance will be as a measure of the actual distance travelled by dispersers. A study on resident wolves suggested that if relocations are taken at 0.5–2 h intervals, multiplying the line segments by a correction factor of 1.3 will give reliable estimates of the actual distance travelled (Musiani, Okarma & Jędrzejewski, 1998). Actual distances travelled by dispersers can reach greater than 10,000 km in a year, as estimated for a yearling female in Scandinavia (Wabakken *et al.*, 2007). However, whether this correction factor can be applied generally to dispersers remains to be tested. Finally, the duration of dispersal also varied among and within study areas (Fig. 3), ranging from 2 days to 38 months. Variability shown in dispersal distance and duration is shaped by the individual, social and environmental factors discussed below (Table 2).

Some studies found that dispersal duration was similar across age classes (Gese & Mech, 1991; Jimenez *et al.*, 2017), whereas dispersal distance was age dependent. Young wolves often travel longer distances than adults (Gese & Mech, 1991; Wydeven, Schultz & Thiel, 1995; Kojola *et al.*, 2006; Jimenez *et al.*, 2017), probably due to young wolves being easily displaced by larger, older, more experienced and sexually mature dispersing adults. The majority of studies did not detect sex differences in dispersal distance (Messier, 1985; Mech, 1987; Fuller, 1989; Gese & Mech, 1991; Boyd *et al.*, 1995; Ballard *et al.*, 1997; Mech *et al.*, 1998; Wydeven *et al.*, 1998; Boyd & Pletscher, 1999; Kojola *et al.*, 2006; Jimenez *et al.*, 2017) nor dispersal duration (Gese & Mech, 1991; Jimenez *et al.*, 2017). However, some studies (Peterson, Woolington & Bailey, 1984; Caniglia *et al.*, 2014; Wabakken *et al.*, 2015; Sanz-Pérez *et al.*, 2018) reported longer dispersal distances for males, resembling the pattern observed in many mammals, which has been suggested to reduce inbreeding (Greenwood, 1980; Long *et al.*, 2008).

Several studies discussed the influence of social and environmental factors on the duration and distance of dispersal events. In particular it has widely been stated that a high density of wolves in a population may lead to longer dispersals in both duration and distance in search for suitable vacant habitats (Van Ballenberghe, 1983; Messier, 1985; Mech *et al.*, 1998; Blanco & Cortés, 2007; Wabakken *et al.*, 2015). However, supporting evidence is speculative, and some studies observed the opposite trend (Jimenez *et al.*, 2017). Another factor believed to trigger long dispersals that remains to be empirically tested is a failure to find unrelated mates nearby (Mech, 2020).

Human-caused mortality inarguably shortens distances and duration of dispersal events. This is because dispersers are particularly vulnerable to human-caused mortality, which is additive to natural mortality (Creel & Rotella, 2010; Murray *et al.*, 2010). Important implications are reduced population gene flow and increased population genetic structure (Rick *et al.*, 2017). Moreover, it seems plausible that individuals attempt to occupy nearby vacant territories created by removing entire packs in preference to making longer dispersals. However, the extent to which dispersers immigrate into groups affected by human-caused mortality remains far from clear (see Section III.3). Another factor that has been proposed to shorten dispersal distance is a high degree of habitat modification by humans (Blanco & Cortés, 2007). However, it is difficult to separate such landscape effects from mortality risk effects.

Disentangling the effects of social and environmental factors on the length of dispersal events represents a fertile ground for future research. Conclusions are based on beliefs or, at best, simple analyses with the variable of interest. We require a robust analysis that simultaneously tests the

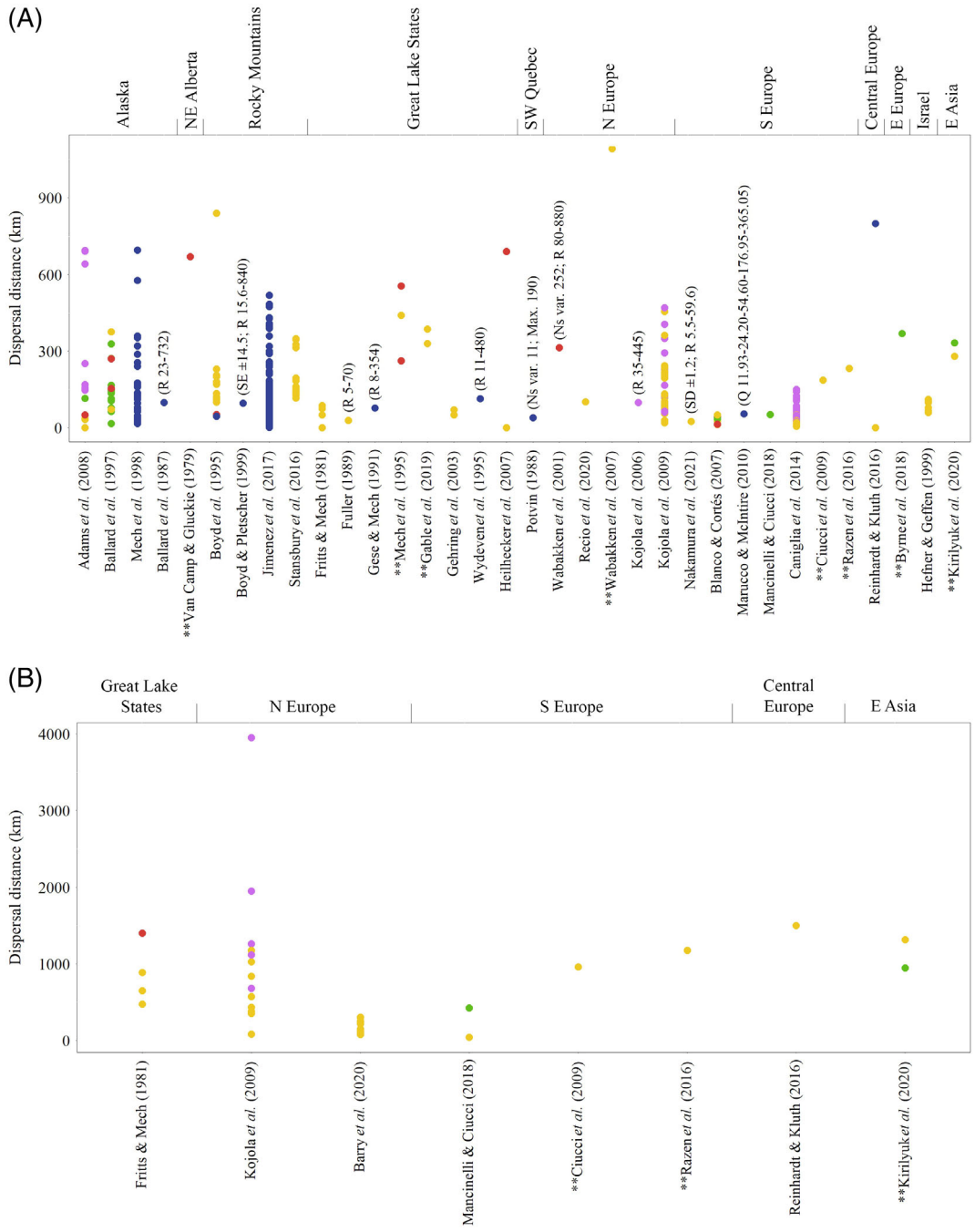

Fig 2. Distance of dispersal events documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range. (A) Straight-line distances of dispersal events. (B) Sum of straight-line distances between successive relocations of dispersers; the frequency of relocations varied from 10 min to 5 days. Symbols of different colours indicate the locations for which distances were measured: from the initial pack territory to the territory where the disperser established for potential reproduction (yellow), to the mortality location of the individual while dispersing (red), or to an unspecified outcome among the two previous ones (blue). Note that these distances correspond to dispersal events that were monitored from the beginning to the end of dispersal. Green symbols are distances measured for partially monitored dispersal events, either because monitoring started when individuals were already dispersing or because distance was measured to the last known location of the individual while dispersing. Purple symbols are distances that lacked information on whether they corresponded to fully or partially monitored dispersal events. A double asterisk (**) shows studies focused on what the authors considered to be long-distance dispersal events. Variability corresponding to mean values is shown in brackets: R, range; SE, standard error; Q, quantiles; Ns var., statistic of dispersion not specified in the original study; Max., maximum. Distances per age and sex classes are available in Table S2.

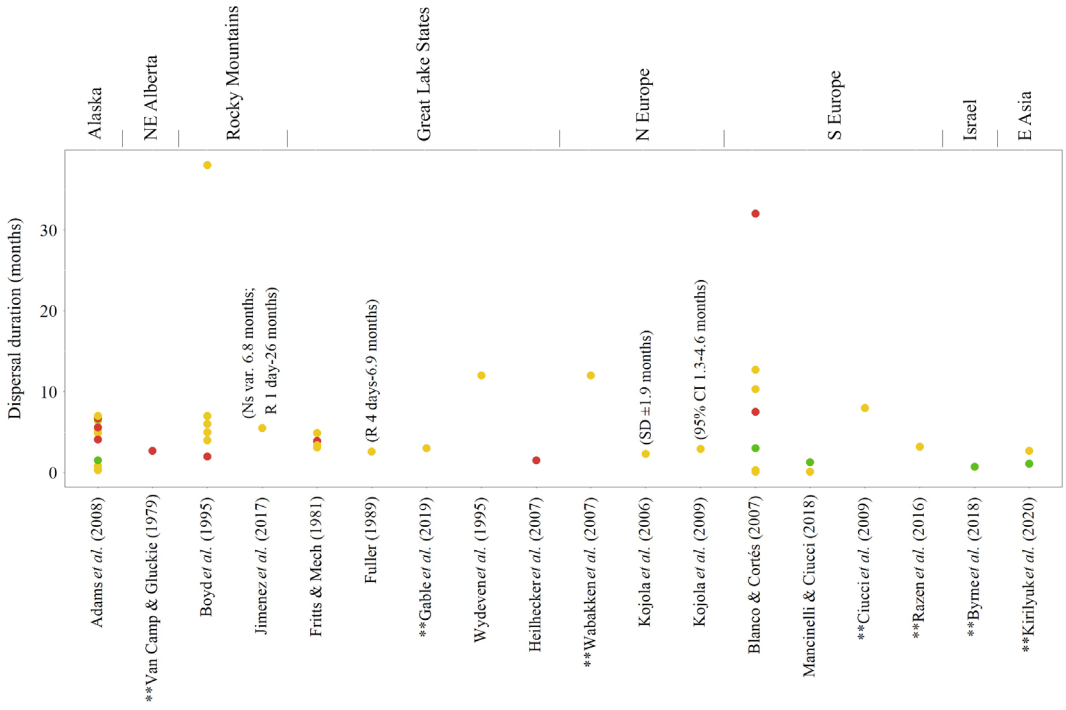

Fig 3. Duration of dispersal events documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range. Symbol colour indicates the locations for which durations were measured: from emigration from the initial pack territory to the establishment in a territory for potential reproduction (yellow), or to the mortality of the individual while dispersing (red). Note that these durations correspond to dispersal events that were monitored from the beginning to the end of dispersal. Green symbols are the durations measured for partially monitored dispersal events, either because monitoring started when individuals were already dispersing or because duration was measured to the last known location of the individual while dispersing. A double asterisk (**) shows studies focused on what the authors considered long-distance dispersal events. Variability corresponding to mean values is shown in brackets: R, range; SD, standard deviation; 95% CI, 95% confidence interval; Ns var., statistic of dispersion not specified in the original study. Durations per age and sex classes are available in Table S2.

influence of biologically meaningful determinants and identifies the confounding factors that may have misled interpretation to date.

(3) Settlement stage – dispersal success

We extracted numerical data on dispersal success from 30 out of 34 articles (Table S3). In a mean of 30.5% (SD = 29.2; range R = 0–87; N = 20 studies with $N > 6$) of the dispersal events per study it was unknown or not specified whether the disperser succeeded in establishing in a territory or died before establishment. Of the dispersal events with known fate, a mean of 76.9% (SD = 23.6; R = 31–100; N = 21 studies with $N > 6$) per study ended with the disperser establishing in a territory *versus* a mean of 23.1% in which the disperser died before establishment. It is not known what proportion of the dispersal events whose fate was unknown or not specified corresponded to mortality, in particular to poaching events. Poaching is an important source of wolf mortality (Treves *et al.*, 2017; Sunde *et al.*, 2021) and investigating the extent to which it affects dispersers is paramount to reducing uncertainty in dispersal estimates. Data on pairing, denning and reproductive status corresponding to each dispersal event were not available or not easily derived from the information provided and so no reliable conclusions can be drawn. The following individual, social and environmental factors influence dispersal success in establishing in a territory, pairing, denning and reproducing (Table 2).

Some studies found that the age of the wolf at dispersal did not influence its success at establishing in a territory, whereas success at pairing and denning was higher for adults, intermediate for yearlings and lower for pups (Gese & Mech, 1991; Jimenez *et al.*, 2017). Cases of successful reproduction have not been documented for pups and they are rare for yearlings (Wikenros *et al.*, 2021). Success at denning for dispersers aged ≥22 months increased with age (Jimenez *et al.*, 2017). Success at denning was twice as high for females than for males (Jimenez *et al.*, 2017). This is likely because females more frequently paired with another dispersing wolf to form new packs than joined an existing pack, whereas males did so with equal frequency (Jimenez *et al.*, 2017). Success at denning was 11 times higher for wolves that formed new packs (Jimenez *et al.*, 2017). Another individual determinant is the coefficient of inbreeding. Inbred wolves showed lower success at pairing and reproducing (Åkesson *et al.*, 2016).

Success at denning for dispersers that settled in a colonizing population declined by 10% for every unit increase in pack density (i.e. the number of packs present in the study area per unit study area) (Jimenez *et al.*, 2017). Rate of

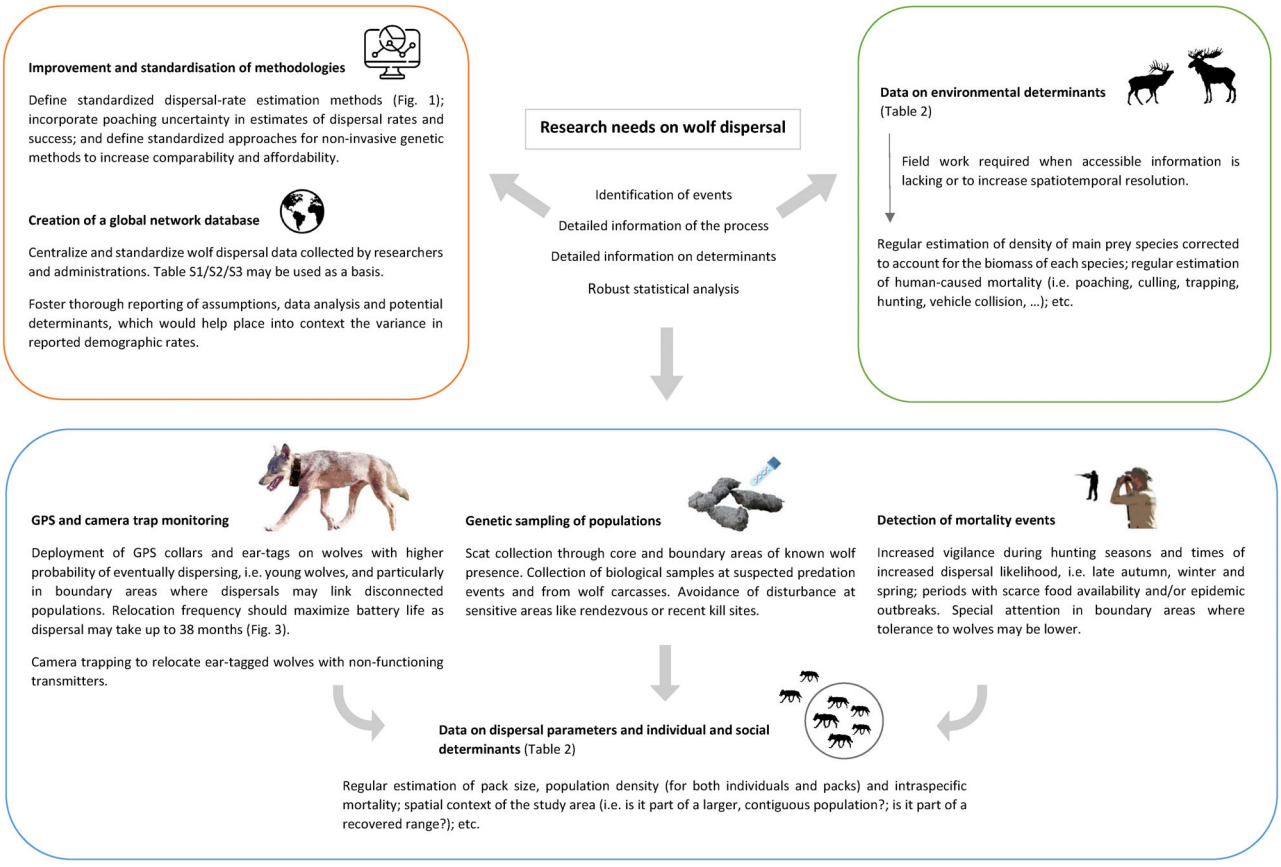

Fig 4. Research needs to improve current understanding of the dispersal process in grey wolves. Recommendations are grouped into three types: deep studies of wolf populations (blue box), related environmental data (green box) and improvement of data collection and management (orange box). Researchers and administrations should collaborate proactively to implement the described tasks successfully. Icons downloaded from: flaticon, http://www.flaticon.com (Freepik: computer, earth and DNA tube); pngwing, http://pngwing.com (elk and hunter); and freepng, http://freepng.es (moose). Wolf scat picture: Héctor Ruiz-Villar; wolf picture: Ezequiel Martínez Vera.

mortality did not influence success at denning and was discarded as confounding factor. Wolves in low-density areas also showed high success at pairing (Fritts & Mech, 1981) and high success at establishing in a territory (Blanco & Cortés, 2007). These results contrast with the Allee effect, which predicts a reduced probability of finding mates and establishing new breeding units at low densities (Courchamp, Berec & Gascoigne, 2008). Changes in wolf density in an area with high wolf occupancy were unrelated to dispersal success at pairing, establishing in a territory or denning (Gese & Mech, 1991).

Little is known about the circumstances that trigger immigrant acceptance into existing packs. Newcomers often enter as replacements for lost breeders. This applies especially to males whereas successors of lost breeding females are commonly related subordinates (Jędrzejewski *et al.*, 2005; Vonholdt *et al.*, 2008; Caniglia *et al.*, 2014). However, some newcomers enter as subordinates that eventually may become breeders (Mech *et al.*, 1998; Jimenez *et al.*, 2017). Death of breeding pack members but also other circumstances may trigger immigrant acceptance. Small packs may be more prone to accepting unrelated individuals. Additional non-breeding members would help to maintain group size and offspring recruitment (Ausband *et al.*, 2015). Accordingly, Ballard, Whitman & Gardner (1987) showed that the mean size of packs to which wolves immigrated was smaller than that from which they emigrated. By contrast, Bassing *et al.* (2020) found that the proportion of immigrants within groups in a protected population was low and did not change when pack size and offspring recruitment declined after hunting and trapping began. In addition, they documented similarly low immigrant acceptance in a population hunted and trapped at a higher rate. Social constraints of groups may commonly limit immigration if breeding pairs persist. How human-caused mortality levels affect dispersal success has been poorly studied apart from its effects on immigration into groups. However, an overall reduction in success of dispersers can be expected from an increased mortality risk. For instance, Kojola *et al.* (2006) observed that all dispersers that travelled through areas subject to high hunting levels were killed before they succeeded in reproducing.

Finally, dispersal distance, i.e. a behavioural decision taken during transience, also influences dispersal success. In an established population, the chances of establishing a new

territory/being accepted into an existing one decreased with distance from the initial territory whereas the chances of dying increased (Gese & Mech, 1991). Moreover, although denning occurrence in new territories may not depend on distance (Jimenez *et al.*, 2017), success at reproduction was higher for wolves that dispersed short distances in an expanding population (Caniglia *et al.*, 2014).

IV. CONCLUSIONS

(1) There is a surprisingly high variability within and among study areas for dispersal parameters related to all three stages of grey wolf dispersal – dispersal rate, direction, distance and duration, and success. This large variability is due to multiple individual, social and environmental determinants (Table 2), but also to numerous methodological research issues.

(2) Age and sex are well-known key individual determinants of dispersal at all stages. Dispersal rate is similar for yearlings and adults, and negligible for pups. Dispersal distance and overall success at settlement decrease and increase respectively with age. Sex differences only occur in some populations, with males showing higher rates of dispersal, longer travel and joining existing packs as often as forming new ones.

(3) Population density is the main determinant of the variability in the annual dispersal rate within populations, and data suggest that dispersal rate peaks at both ends of the gradient of population density. Population density is also crucial at settlement, with low densities resulting in higher success at pairing, territory establishment and denning, and with a negative relationship between pack density and denning probability in colonizing populations.

(4) Among the environmental determinants of dispersal, human-caused mortality reduces distance, duration and success of dispersal events. Dispersers are particularly vulnerable to human-caused mortality, and its additivity to natural mortality evidences these negative effects. In addition, dispersers avoid interaction with humans; motorways, urban centres and agricultural areas represent important barriers to wolf dispersal in many areas.

(5) The following methodological issues make it difficult to obtain robust estimates of dispersal parameters and robust inferences about dispersal patterns and their determinants: (*i*) variation in field monitoring and statistical methods used to estimate dispersal parameters; (*ii*) ignoring the dynamics of wolves adjacent to studied local sites when inferring the dynamics of entire populations; (*iii*) non-detection of poached dispersers; (*iv*) incomplete monitoring of dispersal events; (*v*) monitoring biased towards short-distance movements; (*vi*) failure to provide complete and detailed information of each monitored dispersal event; and (*vii*) non-accounting for potential confounding factors and key biologically meaningful determinants when analysing the variability of dispersal parameters. These issues lead to substantial knowledge gaps on all aspects of dispersal that should be addressed in future research (Fig. 4).

(6) Researchers should collect information on dispersal parameters together with valuable data on potential determinants, and make such data accessible for future studies (Fig. 4). This would allow for a meta-analysis and a more robust knowledge of the influence, relative importance and interactions between the different determinants, and thus to an overall better understanding of the dispersal process in grey wolves.

V. ACKNOWLEDGEMENTS

During this research, E.R., A.M.-G., A.F.-G. and M.Q. were financially supported by the Project CGL2017-83045-R financed by the Spanish Ministry of Science and Innovation and Universities, the Agencia Estatal de Investigación (AEI) and the Fondo Europeo de Desarrollo Regional (FEDER, EU). A.M.-G. was supported by the Predoctoral Fellowship PRE2018-086102. We thank Héctor Ruiz-Villar for stimulating discussions and helpful suggestions. We also thank two anonymous referees and the journal editors for their positive feedback.

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VII. Supporting information

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

Fig. S1. Spatial location of the reviewed studies (except for seven review articles with no specific spatial location) on grey wolf dispersal across the distribution range of the species (according to the IUCN *Red List of Threatened Species*; Boitani, Phillips & Jhala, 2018) drawn on a worldwide map.

Table S1. Dispersal rates documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range.

Table S2. Distance and duration of dispersal events documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range.

Table S3. Fate of dispersal events documented in the scientific literature (up to September 2021) for the grey wolf across its distribution range.

(*Received 2 June 2021; revised 7 October 2021; accepted 8 October 2021; published online 18 October 2021*)