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Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain

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Canis lupus; grey wolf; dispersal; pack formation; tenure; mortality.

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Abstract

Wolf *Canis lupus* dispersal, social structure and mortality have been extensively studied in natural and semi-natural areas of North America and northern Europe but have never been assessed in agricultural areas. From 1997 to 2004, 14 wolves (11 in a wolf-saturated area and three in a low-density area) were radio-collared with long-lasting transmitters in a Spanish agricultural area containing a high-human-population density, a dense network of roads and a shortage of wild ungulates. The wolves mainly feed on an overabundance of livestock carrion. Nine wolves (one of them, three times) dispersed during the study period. The mean age and distance of natal dispersal were 24.8 months and 32 km. The natal dispersal period was much longer in wolves radio-collared in the saturated area (mean >14.6 months) than in the low-density area (<1 month). All three of the dispersers living in the low-density area, and two of the six dispersers in the saturated area settled and bred during the study. The average tenure of six breeders was 4.5 years. The radio-collared wolves spent 72% of the monitoring time living in packs and the rest living in pairs, as dispersers or as peripheral wolves, but the percentage of loners was much higher in the saturated (33.5%) than in the low density (1.6%) areas. The overall annual mortality was 18% (lower than in most populations studied in less modified habitats), but lone wolves had a significantly higher mortality than members of packs and pairs. Nine wolves died during the study, none of them due to natural causes. In general, our results are very similar to those obtained in less modified habitats, except for the dispersal distance, which was much shorter than in other studies. We suggest that barriers and habitat constraints may reduce dispersal distances in our study area.

Introduction

Dispersal is the principal means by which maturing grey wolves *Canis lupus* leave their natal packs, reproduce and potentially expand their population's geographic range (Fuller, Mech & Cochrane, 2003). In social animals such as wolves, dispersal is an important mechanism for population regulation (Lidicker, 1975), and is likely to influence survival (Waser, 1996).

Grey wolf dispersal has been studied extensively in North America (see review in Fuller *et al*., 2003). In Europe, the only dispersal data available are from Scandinavia (Wabakken *et al*., 2001) and Finland (Kojola *et al*., 2006). All these studies have been carried out in wilderness or only partially modified areas, where wolves prey on wild ungulates and there are no obvious barriers to wolf dispersal. Nevertheless, many wolf populations live in close contact with humans in many parts of southern Europe, the Middle East and southern Asia (Boitani, 2003), where habitat characteristics differ considerably from those of the above-mentioned regions. Moreover, considering the recent expansion of wolves in much of their range (Mech, 1995), it is likely that in the future they will increasingly occupy more modified regions.

In Spain, following centuries of severe persecution, wolves reached their lowest point in the 1970s. Subsequently, they were partially protected and the largest remaining population started to increase and expanded southward and eastward (Blanco, Reig & Cuesta, 1992). During the 1980s, wolves appeared in flat, agricultural, treeless and densely inhabited areas with a near-absence of wild ungulates. In these areas, the habitat is patchy and there is a dense network of highways, roads, railways, rivers and transport infrastructures that sometimes act as semi-permeable barriers for wolves (Blanco, Cortés & Virgós, 2005). Wolves mainly feed on livestock carcasses they find in dumps or scattered throughout the countryside, and during most of the study period a surplus of food was available (Cortés, 2001). These habitat conditions may influence dispersal and population dynamics, parameters that have not been documented previously in this kind of habitat.

This paper assesses the dispersal patterns of wolves living in this agricultural area and other parameters related to dispersal, such as social structure and mortality. Our aim is to compare our results with those obtained in the studies carried out during the last 40 years in wilderness and semi-wilderness areas.

Study area

We conducted the study in the provinces of Valladolid, Zamora, Segovia and Ávila, in north-central Spain (Fig. 1). The study area comprises flat, almost treeless agricultural land, with cereal and maize fields providing some cover for wolves during certain seasons. Remnant forests only cover 7 and 26% of the area north and south of the River Duero (which bisects the study area), respectively. These fragmented forest patches are generally privately owned, with restricted public access. Wild boar *Sus scrofa*, the only wild ungulate in the area, is common in the remnant forests (*c.* 1 animal km^{-2}) but almost absent in agricultural areas (Cortés, 2001). European rabbits *Oryctolagus cuniculus* are locally abundant and Iberian hares *Lepus granatensis* reach densities of 3.5 individuals km^{-2} in optimal areas (Calzada & Martínez, 1994). The human population (10–40 inhabitants km^{-2}) engages in agriculture and, to a lesser extent, in livestock farming.

Sheep flocks are usually protected by shepherds during the daytime and locked in pens at night, and so damage to livestock is low and people's tolerance of wolves is higher than in other parts of Spain (Blanco & Cortés, 2002).

The main food of wolves in our area is livestock carrion. In 603 scats analysed, livestock carrion comprised 75.3% of the biomass consumed by wolves, and wild boar just 5.7% (Cortés, 2001). Until the end of 2000, most of the carcasses of the livestock that died in the farms were accessible for wolves. In 1999, we interviewed 129 shepherds, who declared that they disposed of the dead livestock in open pits (77.3%) or left them in the fields (8.5%) (Cortés, 2001). In late 2000, bovine spongiform encephalopathy (BSE) was detected in Spain; new laws that obliged farmers to incinerate sheep and cattle carcasses were strictly enforced and carrion pits were progressively closed, and so food availability for wolves started decreasing. In 2003, five of six carrion pits located in the territories of radio-collared wolves were closed. As a consequence, we consider two periods in the study: until the end of 2000, when food was apparently overabundant, and from 2001, when carrion availability started to decrease.

At the beginning of the study, wolves were almost absent south of the river Duero, with appreciable colonization of this area from 1999 onwards. Throughout the whole study period, wolf density was much higher to the north than south of the river Duero, and in 2001 wolf density was estimated at 1.63 and 0.77 packs/1000 km^2, north and south of the river Duero, respectively (Llaneza & Blanco, 2005). North of the Duero, the population is apparently saturated. North of the river Duero, low wolf hunting quotas are allowed whereas to the south of the Duero they are fully protected. Poaching is common on both sides of the river (Cortés, 2001). North of the river Duero, the road density is 0.40 km km^{-2} when considering just paved roads, and 1.53 km km^{-2} when considering 'permanent roads' (Mladenoff *et al.*, 1995; Merrill, 2000).

Methods

From March 1997 to May 2004, we radio-collared 14 wolves in six different packs using the procedure described

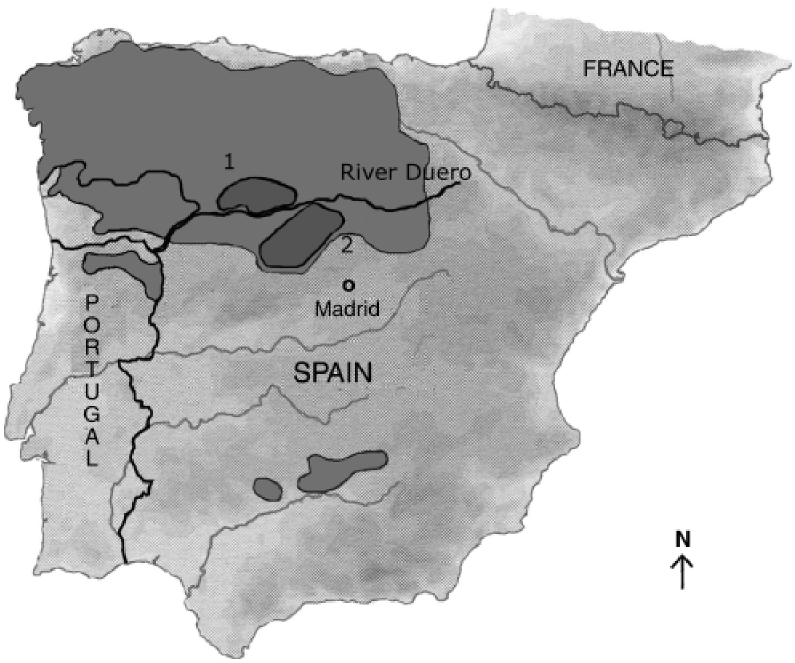

Figure 1 Wolf *Canis lupus* range in Spain (grey) (Blanco & Cortés, 2002) and our study areas (1) to the north and (2) south of the Duero (dark grey).

elsewhere (Cortés, 2001; Blanco *et al*., 2005). Eleven wolves were radio-collared with VHF transmitters (Televilt, Lindesberg, Sweden) whose batteries have an average life of 6 years, two with VHF transmitters (Telonics, Mesa, AZ, USA) with 2–3-year duration batteries and one with a GPS-GSM transmitter (Vectronic, Berlin, Germany) that only lasted 3 months. In addition, the radio-collared wolves were sometimes observed or killed after their batteries expired, and this information was integrated into our data. Age was estimated by body size and appearance, tooth replacement (Van Ballenberghe & Mech, 1975), tooth wear (Valverde & Hidalgo, 1979; Landon *et al*., 1998; Gipson *et al*., 2000) and date of capture. Wolves were divided into three age categories: pups (<12 months old), yearlings (12–24 months old) and adults (>24 months old). Wolves were located from the ground or aircraft using standard triangulation or homing techniques (Mech, 1983). We also monitored them intensively during all-night sessions (Blanco *et al*., 2005).

Natal dispersal is the movement of an animal from its natal home range to where it reproduces or would have reproduced if it had survived or found a mate. Breeding dispersal or secondary dispersal is the movement of an adult between consecutive breeding sites or groups (Greenwood, 1980; Shields, 1987; Gese & Mech, 1991; Waser, 1996). We assume that wolves <2 years old were captured in their natal home range unless there was evidence to indicate otherwise.

The annual dispersal rate was estimated in two different ways: (1) by dividing the number of dispersers by the wolf-years of monitoring (Gese & Mech, 1991; Mech *et al*., 1998); (2) using the program MICROMORT (Heisey & Fuller, 1985), substituting the event death for the event dispersal, as recommended by Arthur, Paragi & Krohn (1993) and Ferreras *et al*. (2004). This method allows statistical comparisons to be made using the Z statistic proposed by Heisey & Fuller (1985).

Before leaving the area, some dispersers show pre-dispersal forays (Messier, 1985) or spent some time in the periphery of their natal home range. This process is defined as the pre-dispersal period. Similarly, some wolves, after reaching their establishment home ranges, show incomplete site fidelity for some weeks or months before finally settling. This is the settlement period. We defined the total duration of dispersal as the time between the start of dispersal and establishment. The pre-dispersal period was not included in the calculation of dispersal duration unless otherwise specified.

Dispersal distance is the distance between the arithmetic centre of the natal home range, or the capture site, to establishment home-range centre, the mortality site or the last location while dispersing (Maehr *et al*., 2002). The distances of effective dispersals were compared with the average home range width of resident wolves (15 km), which was calculated as the diameter of a 182 km^2 circle (the average area of an adult wolf home range in our study area using the 95% minimum convex polygon method, J. C. Blanco & Y. Cortés, unpubl. data).

Pair formation was confirmed when the target wolf was consistently seen with another wolf during or after the dispersal period. Pack formation was deduced from the presence of three or more wolves showing site fidelity, assessed by observation of the wolves or through elicited howling. Breeding was confirmed by visual observation of the pups or from pups answering to simulated howling (Harrington & Mech, 1982).

To study the social structure of the wolf population, we recognized four categories of social status: (1) pack members, (2) pair members, (3) dispersers (4) peripheral wolves, defined by Mech (1970) as the individuals that rank so low that they avoid the main pack members and stay near the fringes of the pack social centre. Dispersers were recognized as they do not show site fidelity. The three other categories were established by assessing whether the radio-collared wolves were consistently alone (peripheral wolves) or living with other pack or pair members. With this objective we tried to observe the wolves actively, used the simulated howling method and checked tracks in the sand. During the study, we carried out 528 'sit and wait' observation sessions (e. g. at rendezvous sites) and 253 simulated howling trials. The percentage of wolves in each given category was estimated by dividing the sum of those days spent by each radio-collared wolf in the category by the number of radio-days of all categories. The periods in which the social category of wolves was uncertain were excluded from calculations.

We estimated survival rates using the program MICROMORT (Heisey & Fuller, 1985), and we compared survival among social categories using the test proposed by these authors. We assigned mortality dates as halfway between the last known live location and the first indication that the wolf had died, unless carcass evidence indicated otherwise.

Results

Dispersal rate, sex, age, distance and time of dispersal

Between 1997 and 2004, we radio-collared 14 wolves (seven males and seven females) that were followed for a total of 40.6 wolf-years (mean: 34.8 months, range: 3–71 months). Four wolves were followed for 5–6 years and two other wolves for 4–5 years. Nine wolves dispersed during the study period (Table 1; Fig 2), and so the annual dispersal rate was 23.9% (using MICROMORT) or 27.4% (using the method described by Gese & Mech, 1991). Although the annual dispersal rate of males (32.0%) was higher than that of females (16.3%), this difference was not significant ($Z = 1.273$, $P = 0.1014$). Nine of the 11 dispersals (92%) corresponded to natal dispersal and two others (8%) to breeding dispersal. The average age of natal dispersal for seven wolves of known age was 24.8 months (SD = 4.98), 24.5 months for three males and 25.0 for four females. Five wolves dispersed when they were 2–3 years old and the others as yearlings. The minimum average distance of natal dispersal was 32 km ($n = 8$; range: 13–50 km). This is a minimum figure because the signal of one male wolf was lost during dispersal, suggesting a long-distance dispersal.

Table 1 Study period, age, distance and duration of dispersal of the radio-collared wolves *Canis lupus*

Wolf id.[a]	Area[b]	Radiocollaring date	Last data	Monitoring period	Dispersed during the study	Month of natal dispersal	Natal dispersal age (months)	Natal dispersal distance (km)	Predispersal	Dispersal duration
M1	South Duero	01.03.1997	21.12.2002	5 years and 10 months	Yes	January	31	26	No	< 25 days
F1	South Duero	23.04.1997	23.01.2003	5 years and 9 months	Yes	July	26	42	Yes	Unknown
F2	North Duero	10.10.1997	22.02.1998	4 months and medio	No					
F3	North Duero	23.09.1997	23.07.2003	5 years and 10 months	Yes	October	29	13	Yes	10.3 months
F4	North Duero	23.09.1997	23.06.2002	4 years and 9 months	No					
M2	North Duero	08.03.1998	08.09.2002	4 years and 6 months	Yes			50	Unknown	> 12.7 months
M3	North Duero	08.03.1998	23.10.1998	7.5 months	Yes			14	Unknown	> 7.5 months
F5	North Duero	06.05.1998	28.02.2001	2 years and 9.5 months	Yes	August	27	45	No	32 months
M4	North Duero	15.05.1998	22.12.2003	5 years and 7 months	No					
M5	North Duero	31.03.1999	20.08.1999	5 months	Yes	May	24	Lost	No	> 3 months
F6	North Duero	01.04.1999	19.01.2000	8.5 months	No					
F7	South Duero	03.04.2002	10.01.2004	1 year and 9 months	Yes	November	18	30	No	< 9 days
M6	North Duero	31.05.2004	28.08.2004	3 months	No					
M7	North Duero	31.05.2004	23.06.2005	13 months	Yes	Oct–Jan	18.5	36	Unknown	> 7.5 months

[a]M, males; F, females.

[b]North Duero: high wolf density; South Duero: low wolf density.

Dispersal distances were similar for males (31.5 km, $n = 4$) and for females (32.5 km, $n = 4$). Of seven known cases, four natal dispersals started between October and January and the three others in July and August (Table 1).

The natal dispersal process

Pre-dispersal and natal pack abandonment

Two of the nine dispersers were radio-collared when they were already dispersing, and so we do not know whether they had a pre-dispersal process. In the other seven wolves, we did not detect pre-dispersal forays sensu Messier (1985). Nevertheless, two wolves used the peripheral areas of their home range much more frequently in the weeks before their dispersal. The two wolves that avoided the nucleus of the pack before dispersing were F3 and F1. F3, after having attended the breeder's pups throughout summer 1998, left the homesite area in October and occupied the periphery of her natal pack territory for 37 days before dispersing. From summer to the predispersal period, the average distance of the diurnal rest sites between F3 and her pack's breeding female (F4, also radio-collared) increased from 2.2 ($\text{SD} = 2.1$; $n = 27$) to 6.2 km ($\text{SD} = 4.8$; $n = 7$) ($U = 2.619$; $P = 0.002$; Mann–Whitney test). F1 spent 82 days mainly using the periphery of her natal pack territory, between May and July 1997 (breeding season), before dispersing. During this period, only one of the 15 days in which she was located was spent with the pups of the pack; in contrast, during the same period, the radio-collared male M1 (which was probably her brother from the same litter) spent nine of the 20 days in which he was located in his pack homesite (Yates corrected $\chi^2 = 4.44$; d.f. = 1; $P = 0.035$).

Dispersal period

The dispersal period lasted from < 9 days to 32 months. We have recorded two different dispersal patterns. The wolves living in the low-density area south of the river Duero showed very rapid dispersal. Two of them suddenly left their natal pack and when they were detected again, 25 and 9 days after dispersing, they had already settled down in their new areas. The third wolf (F1) also probably showed this pattern, but after leaving her natal area she went missing for several weeks and we cannot be sure. In contrast, in the saturated area north of river Duero, the average dispersal duration was > 14.6 months ($n = 5$) (Table 1). Of the six wolves that dispersed in this area, one disappeared during dispersal and the other five were floating for months or years before settling or dying. Two of them eventually bred, two died before settling and one was still dispersing at the end of the study.

The dispersers that were floating north of the river Duero used different methods to find a vacant territory or be adopted by a pack (Tables 1 and 2). F3 seemed to spiral outward from the natal territory, until she finally established in a corner of it. M2 used a nomadic pattern until he settled

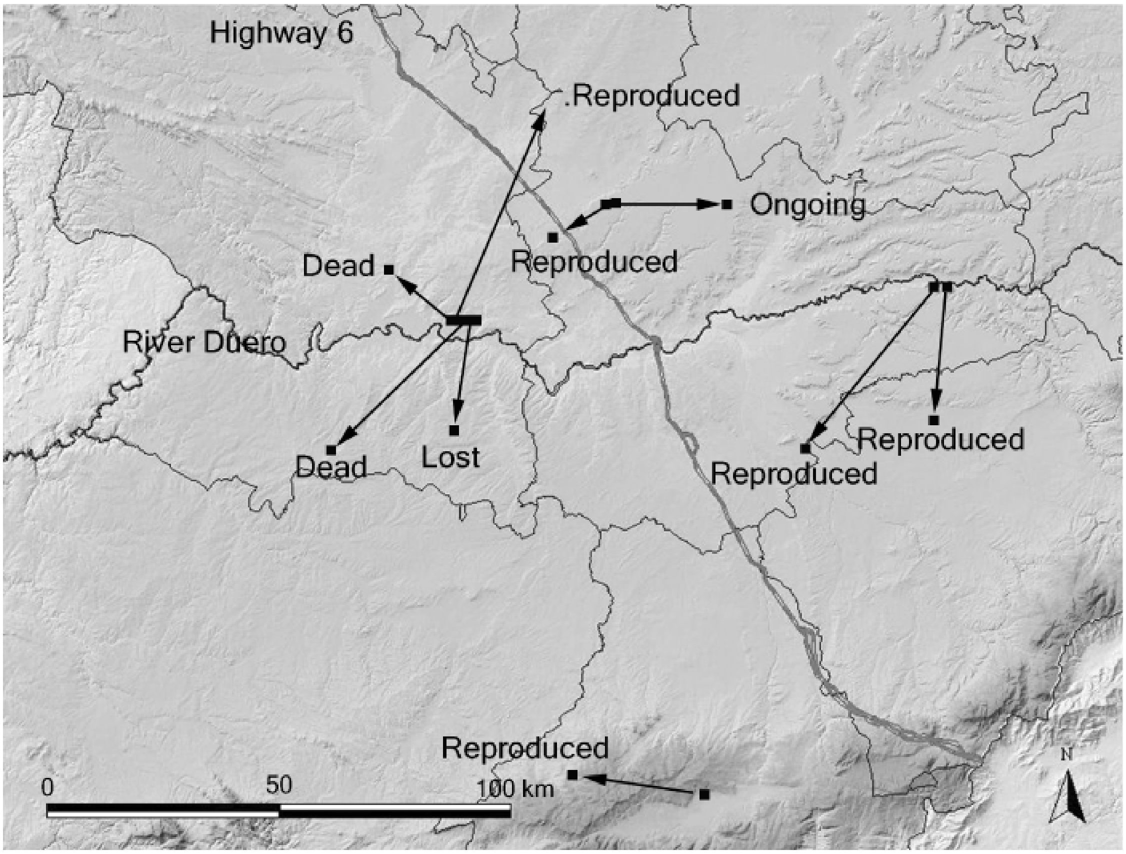

Figure 2 Dispersal of radio-collared wolves *Canis lupus* (1997–2005). The locations where wolves were fitted with transmitters and where dispersers reproduced or died are shown. The river Duero and the Highway 6 are also shown.

Table 2 Pairing and breeding of dispersers, tenure of territorial breeders and fate of all the radio-collared wolves *Canis lupus*

Wolf id.	Pairing	Breeding	Tenure after settling	Fate of the wolf
M1	Unknown		15 months	Battery expired
F1	Paired after dispersal	Bred 4th breeding season after settling	62 months	Killed by car
F2				Illegally poisoned
F3	Paired after dispersal	Bred 2nd breeding season after settling	52 months	Killed by car
F4[a]			> 57 months	Illegally shot
M2	Paired before or during dispersal	Bred 1st breeding season after settling	> 42 months	Battery expired
M3	Did not pair	Died before breeding		Killed by car
F5	Did not pair	Died before breeding		Illegally shot
M4[a]			> 90 months	Legally shot
M5	Unknown	Unknown		Lost during dispersal
F6				Illegally shot
F7	Paired after dispersal	Bred 1st breeding season after settling	14 months	Killed by dogs
M6				Collar failure
M7	Paired before or during dispersal	Did not breed 1st breeding season after dispersal		Ongoing monitoring

[a]Radio-collared when they were territorial breeders.

in a vacant territory. M3 showed a nomadic pattern but mainly shifted between two packs. And F5 explored specific areas and moved to contiguous ones every few months (Fig. 3). Floaters did not avoid other packs: F5 and M2 were each detected in the core areas of three known wolf packs, F3 and M3 in that of two packs and M7 in that of one pack.

The settlement process

Of the nine wolves that started the dispersal process, two died during their dispersal, one disappeared and one was still dispersing at the end of the study. Four of the five wolves that established successfully, settled just after

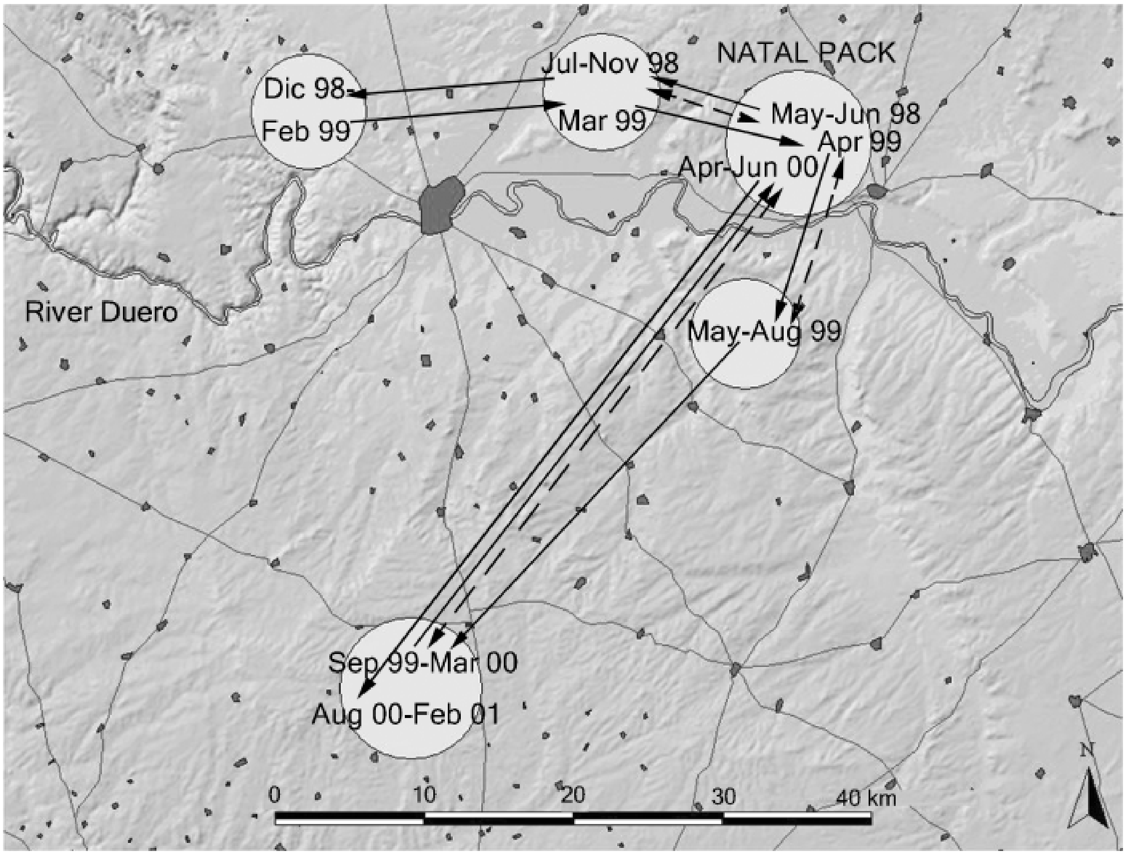

Figure 3 Dispersal of F5 (May 1998–February 2001). She successively occupied five home ranges and died before settling. The broken lines indicate back and forth movements.

arriving and were not detected in their natal home ranges anymore. For the fifth wolf (F3), the settlement was a progressive process that lasted 7.5 months. During this time, in eight of the 27 locations (29.6%) she had returned to visit her natal territory.

Pairing, pack formation, breeding and tenure after settling

We have data on pair formation on five of the nine dispersers: two males (M2 and M7) paired before or at the beginning of their dispersal, and three females (F1, F3 and F7) paired after or at the end of the dispersal. Of the five successful dispersers, three of them formed their own pack: M2 and F7 reproduced in the first breeding season after settling and F3 in the second breeding season. Two other dispersers joined existing packs: F1 formed a pair in an existing pack, bred 4 years after settling and formed a new pack (the former one split into two). M1 joined another pack and then dispersed twice in subsequent years.

The different dispersal success had distinct consequences for the population trends on the different sides of the river. The three wolves radio-collared south of the river Duero dispersed and eventually formed their own packs, but only two of the six wolves (33.3%) that dispersed north of the Duero formed a new pack. The characteristics of the newly formed territories were also very different on both sides of the river. South of the river Duero, the three new packs formed at the edge of the distribution area, in areas not occupied by other wolves and of much better quality habitats than the two packs formed in the north. Agricultural and other very modified habitats formed 21, 68 and 19% of the three new packs' territories to the south of the Duero, and 78 and 99% of those north of the Duero. North of the river, one of the new packs was formed by budding. F3 set up a territory occupying the worst-quality portion of her mother's (F4) territory, which was also bisected by a four-lane fenced highway (Blanco *et al*., 2005). The second pack north of the Duero was formed by M2, who carved out a territory in a practically treeless area after floating nomadically for more than a year.

Seven radio-collared adult females were monitored for an average of 3.2 years (range: 0.5–5.9 years) until they died, and their complete reproductive histories are known. Three adult females never reproduced. The other four females bred once, twice, four and $\geq$six times, respectively, during their lifespan.

Four of the five wolves that settled after dispersing retained their territory until they died, or until the radio-collar battery expired (Table 2). In addition, two wolves that

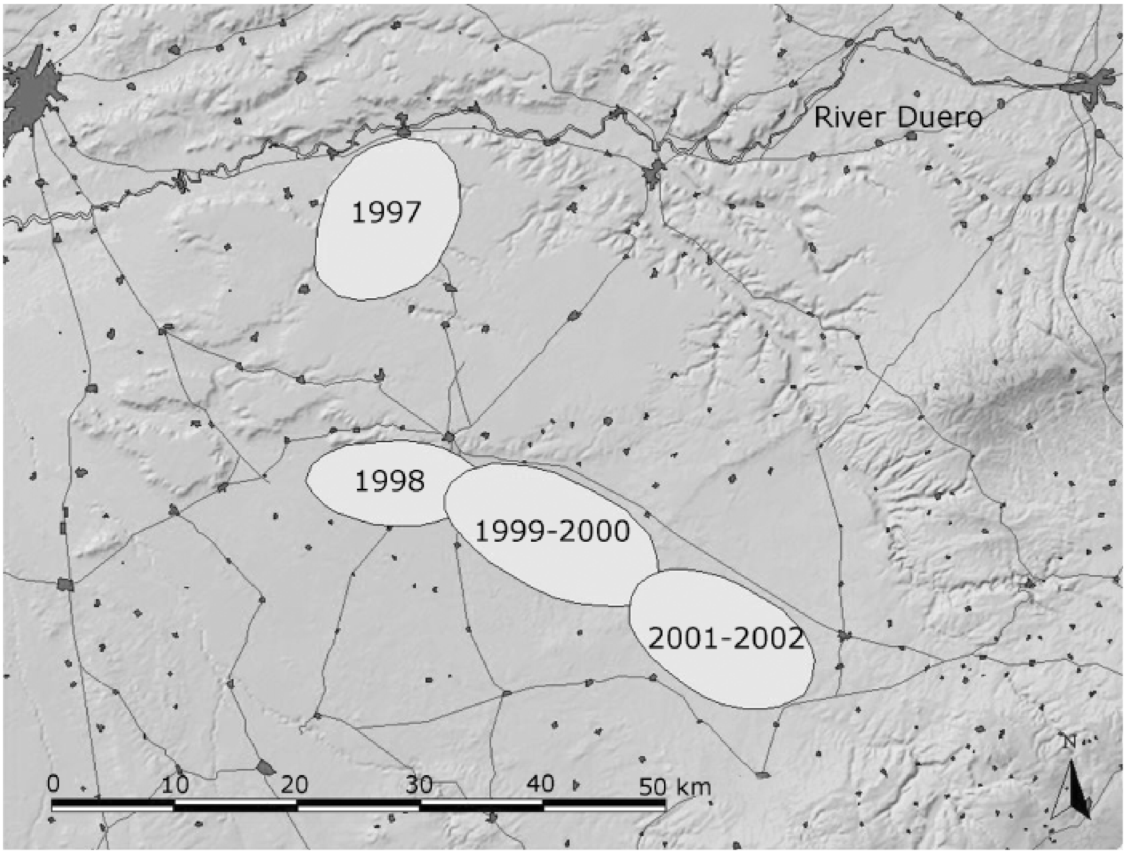

Figure 4 Dispersal of M1. In 1998, he dispersed from his natal home range (natal dispersal), and in subsequent years he dispersed again twice (breeding dispersal).

were radio-collared when they were already territorial breeders (M4 and F4) retained their territory until they were shot. The average recorded tenure of these six breeders was 4.5 years (range: 1.1–7.5 years).

Breeding dispersal

Only one case of breeding dispersal was detected. M1 dispersed from his natal pack in January 1998 (when he was about 31 months old) and joined another pack 26 km away. In October 1999, he moved to a contiguous territory 17 km away and stayed there for 2 more years. In 2001, he moved again to another contiguous territory 18 km away from the last one and remained there at least until 2002, when his battery expired. In the two breeding dispersals, he moved a similar distance to the diameter of an average territory (15 km). These breeding dispersals were gradual and the new territories overlapped the previous ones (Fig. 4).

Social structure and mortality

From 1997 to 2004, we made 267 observations of the radio-collared wolves and other members of their packs, performed 253 sessions of simulated howling close to them and wolves replied 88 times (34.8%). At the end of the study, the radio-collared wolves were found 72% of the observations living in packs and the rest living in pairs, as dispersers or as peripheral wolves. (Table 3).

The overall annual mortality rate was 18%, but it varied depending on social category. Members of packs and pairs showed the lowest mortality rates and dispersers and peripheral wolves had the highest (Table 4). Lone wolves (i.e. dispersers plus peripheral wolves) had a significantly higher mortality (44% annual) than members of packs and pairs (12%) ($Z = 1.6803$, $P = 0.046$). Nine radio-collared wolves died during the study (Table 2), none of them due to natural causes. Illegal killing (44.4%) and traffic kills (33.3%) were the main causes of mortality. One wolf was apparently killed by dogs on a cattle-rearing estate.

Discussion

Wolf dispersal occurs normally once in the life of the animal and is difficult to detect using normal VHF radiocollars, which only have a 1–2-year lifespan (Mech, 1987). However, we used radiocollars with a battery life of 6 years, which allowed us to follow some of the wolves throughout the greater part of their lifespan. In fact, six wolves were followed for 4–6 years, and nine of the 14 dispersed while their radiocollar was active.

In addition, our study differs in several ways from those undertaken previously on wolves. The area is highly modified, had (at least during the majority of the study period) a food surplus deriving from livestock carrion, it is a highly fragmented landscape, with few woodland patches where wolves can breed safely, and also has a considerable number of roads and other man-made barriers (Blanco *et al*., 2005). The road density north of the river Duero is 1.53 km km^{-2}, that is, the highest ever recorded for a wolf population (Merrill, 2000). Several studies carried out in North America in the 1980s suggested that wolf populations could not survive in areas with road densities >0.58 km km^{-2} (Thiel, 1985; Jensen, Fuller & Robinson, 1986; Mech *et al*., 1988). Thus, the conditions of our study area contrast markedly with the studies carried out in North America and in northern Europe where the forested habitat is continuous, the wolves feed on natural prey and there are no obvious barriers to their dispersal.

Table 3 Percentage of radio-days that the radio-collared wolves *Canis lupus* spent in packs, pairs, as dispersers or as peripheral wolves in different periods of the study

	Pack	Peripheral	Disperser	Pair
March 99	67.2	8.8	25.0	0.0
March 01	53.0	9.2	23.5	14.3
March 03	71.2	5.3	13.7	9.8
March 05	72.2	4.9	12.7	10.2

Table 4 Annual mortality rates of radio-collared wolves *Canis lupus* (Heisey & Fuller, 1985)

Social category	Radio-days	Deaths	Mortality rate	95% CI
Overall	14763	8	0.18	0.059–0.285
Pack	10051	4	0.14	0.003–0.250
Pair	1694	0	0	0.000–0.000
Disperser	1952	2	0.31	0.000–0.591
Peripheral	1066	2	0.50	0.000–0.805

CI, confidence interval.

Dispersal patterns and success

Despite these differences, our results were very similar to those studies undertaken in less modified habitats, except for the dispersal distance. The dispersal rate in this study (23.9–27.4%) is very similar to the average dispersal rate for eight studies reviewed by Fuller *et al*. (2003, p. 179) in North America (25.4%), and closely approaches the 28% annual rate found by Mech *et al*. (1998) in the wilderness location of Denali National Park (Alaska), which has characteristics almost completely different from those in our study area. Similar to most other studies, we found no sex-biased dispersal rate (Mech & Boitani, 2003). Regarding dispersal age, five of the seven known-age wolves in our study dispersed when between 2 and 3 years old, and the other two as yearlings. The last two cases dispersed after the closure of carrion pits when the food surplus had disappeared. The last two cases may be evidence of dispersal due to resource competition, and the rest dispersal due to mate competition (Gese, Ruff & Crabtree, 1996). In most other studies, wolves dispersed as yearlings (Mech & Boitani, 2003), but the dispersal age was delayed when food was abundant (Ballard, Whitman & Gardner, 1987; Mech *et al*., 1998; Boyd & Pletscher, 1999), as occurred in our study (Table 5).

In contrast, the mean dispersal distance in our study (32.0 km) was 2.4–7 times smaller than that of wolves in less modified habitats of North America and Europe (Table 5). A probable cause of these shorter dispersal distances is the fragmentation of the habitat and the presence of highways, rivers, transport arteries and other barriers typical of habitats with high human densities (Blanco *et al*., 2005).

Table 5 Dispersal data from various studies

		Mean age (months)			Mean distance (km)			
Study area	*n*	Males	Females	Both sexes	Males	Females	Both sexes	References
Spain	9	24.5	25.0	24.8	31.5	32.7	32.0	This study
North-west Minnesota	8						20–390	Fritts & Mech (1981)
North-east Minnesota	75			18.6	88	65	77	Gese & Mech (1991)
Wisconsin	16				65	144	114	Wydeven, Schults & Thiel (1995)
South-central Alaska	38	30	33		84	114		Ballard *et al.* (1987)
Alaska	21				154	123		Ballard *et al.* (1997)
Rocky Mountains	17	33	23	27	152	264		Boyd *et al.* (1995)
Rocky Mountains	31			35.7	113	78	96.3	Boyd & Plestcher (1999)
Denali National Park	56	30	28				133	Mech *et al.* (1998)
Scandinavia	15				323	123		Wabakken *et al.* (2001)
Finland	50			13.5	109	99	98.5	Kojola *et al.* (2006)
Israel	7						50–150	Hefner & Geffen (1999)
Yellowstone National Park	30			25				Mech & Boitani (2003)

Landscape constraints seem to be the reason why carnivore populations studied in very modified habitats have shorter dispersal distances than those living in undisturbed areas (Maehr *et al*., 2002; Ferreras *et al*., 2004).

In general, the dispersal process in our study area fits into the pattern described for other wolf studies. In areas of low wolf density with many vacant territories, the dispersal period is short, but in saturated wolf habitats the dispersal period is longer and the dispersal success is lower (Fritts & Mech, 1981; Messier, 1985; Gese & Mech, 1991). In our study, the three wolves that dispersed in the low-density area south of the river Duero found a vacant territory or were adopted by a pack a few days or weeks after leaving their natal territory. In contrast, in the saturated area north of the river Duero, the average dispersal duration of five wolves was 14.0 months, and only two of them eventually secured a territory and reproduced. The duration of dispersal in this saturated population is much greater than the mean dispersal duration recorded by Gese & Mech (1991) in Minnesota (4.1, 2.0 and 2.9 months for pups, yearlings and adults, respectively) and is even longer than the maximum dispersal duration (12 months) of the 75 dispersers followed by these authors.

Some authors found that dispersers frequent areas along the interstices among territories (Rothman & Mech, 1979; Fritts & Mech, 1981; Meier *et al*., 1995) but other authors have not observed this pattern (Messier, 1985; Boyd *et al*., 1995). In our study, five of the floaters dispersing north of the river Duero were detected once or several times visiting other packs' homesites. On one occasion, we even located the floater M2 in summer together with the pups of another pack with radio-collared wolves. In other areas, trespassers are frequently killed by territory owners (Mech, 1977; Mech *et al*., 1998). It is possible that the food surplus in our study area results in the wolves not needing to vigorously defend their territories against trespassers, as suggested by Boyd *et al*. (1995).

As a consequence of the different dispersal success on both sides of the river (3/3 south and 2/6 north of the river), the population grew rapidly in the south during the study period, increasing from three packs detected in 1997 to 20 packs in 2001 (Blanco *et al*., 2005; Llaneza & Blanco, 2005) but north of the Duero the population did not obviously increase during the same period.

Solitary wolves and mortality

Another consequence of the different dispersal patterns on both sides of the river is the difference in the percentage of lone wolves. The three wolves radio-collared south of the river Duero were found as loners (dispersers plus peripheral wolves) 1.6% of the observations (13.3 wolf-years' monitoring) and the rest of the time as territorial wolves living in packs or in pairs. In contrast, the 11 wolves radio-collared in the saturated population north of the Duero were found as loners 33.5% of the observations (27.3 wolf-years' monitoring). The reasons for the high percentage of loners north of the river Duero might be the semi-permeable river Duero barrier (Blanco *et al*., 2005; Fig. 1), the food surplus, which delays dispersal, and the poor vegetation cover, which may limit breeding possibilities and formation of new packs. These characteristics are relatively rare in the other areas where wolves have been studied and as a result the percentage of loners found in our population north of the river Duero (33.3%) is higher than that in other studies in less modified habitats. Fuller *et al*. (2003), in an extensive review, concluded that the average percentage of non-resident individuals in North American studies was 12% (range: 7–20%).

The high percentage of loners has several management consequences. On the one hand, they are a buffer for a population, making it less vulnerable to exploitation as they are adult individuals that can quickly replace breeders when these die (Fuller *et al*., 2003). In addition, floaters are undetectable without extensive radiotracking, and so they form a 'shadow population' (Rohner, 1997), which is almost impossible to calculate in the population surveys such as those that are carried out in Spain. These surveys are based on the detection of pups in summer but radio-tracking is rarely used and snow is almost lacking in winter (Blanco & Cortés, 2002; Llaneza & Blanco, 2005).

Surprisingly, the annual mortality rate (18%) in our area was lower, and the tenure of the breeders (4.5 years) higher than in the wilderness of Denali National Park (mortality, 27%; tenure, 4 years: Mech *et al*., 1998). In Denali, most wolves died when killed by other wolves, while in our area all mortalities were caused by humans, except for one wolf, which was apparently killed by dogs. None of our wolves died from natural causes. In our area, the mortality due to humans perhaps compensates for the natural mortality, the food surplus may reduce intraspecific competition and the habitat conditions may be more predictable than in the protected, natural habitats of Denali National Park or Isle Royale (Michigan) where food availability varies according to changes in the severity of the winter (Mech *et al*., 1998; Post *et al*., 1999).

In our study, loners had a higher mortality rate than the territorial wolves integrated in packs and pairs, as occurs in other areas. In Minnesota, Mech (1977) also reported that the annual mortality of territorial adults (18%) was much lower than that of loners (34%), and other studies have shown that dispersers suffer a higher mortality than resident individuals (Peterson, Woolington & Bailey, 1984; Messier, 1985; Fuller, 1989; Pletscher *et al*., 1997). Both peripheral wolves and dispersers are low-ranking individuals and are likely forced to occupy the worst areas. In our study area, the human-caused mortality is the proximate cause of the wolf population regulation, but intraspecific competition appears to be the ultimate factor responsible for this regulation.

The overall annual mortality in our area was very low compared with other studies. Other wolf populations with 15–20% annual mortality rates showed 16–49% annual rates of increase (see the review in Fuller *et al*., 2003). The same occurred in our study area. During 1988–2001, in the whole region of Castile and Leon, wolf density obviously increased in some areas and the range expanded by 35% (from 57 000 to 77 300 km^2) (Llaneza & Blanco, 2005). Although we lack accurate data on wolf numbers, these figures show an obvious increase in the wolf population. This means that wolves can live and increase without the support of immigrants in an agricultural area with a very high road density, almost depleted of wild ungulates, as long they have other food sources and the human tolerance is high. In our area, the livestock management system meant that losses to depredation are minimal and there are consequently relatively low levels of wolf persecution.

Interestingly, the conditions that were prevalent in the majority of our study area are now changing. After the appearance of BSE towards the end of 2000, the carrion pits have started to be closed and the food availability for the wolves is apparently declining. If this decrease continues, the population dynamic parameters could change and in the near future could result in fewer loners, smaller pack sizes and a general reduction in the wolf population.

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