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Long-Distance Dispersal of a Rescued Wolf From the Northern Apennines to the Western Alps

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ABSTRACT By using Global Positioning System technology, we documented the long-distance dispersal of a wolf (*Canis lupus*) from the northern Apennines in Italy to the western Alps in France. This is the first report of long-distance dispersal of wolves in the human-dominated landscapes of southern Europe, providing conclusive evidence that the expanding wolf population in the Alps originates from the Apennine source population through natural recolonization. By crossing 4 major 4-lane highways, agricultural areas, and several regional and provincial jurisdictions, the dispersal trajectory of wolf M15 revealed a single, narrow linkage connecting the Apennine and the Alpine wolf populations. This connectivity should be ensured to allow a moderate gene flow between the 2 populations and counteract potential bottleneck effects and reduced genetic variability of the Alpine wolf population. The case we report provides an example of how hard data can be effective in mitigating public controversies originating from the natural expansion and recolonization processes of large carnivore populations. In addition, by highlighting the connectivity between these 2 transboundary wolf populations, we suggest that documenting long-distance dispersal is particularly critical to support population-based, transboundary management programs. (JOURNAL OF WILDLIFE MANAGEMENT 73(8):1300–1306; 2009)

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KEY WORDS *Canis lupus*, connectivity, dispersal, Global Positioning System (GPS), Italy, long-range movements, transboundary wolf management, wolf.

Dispersal strongly affects population dynamics, distribution, gene flow, spatial and social organization, as well as colonization and rescue effects (Howard 1960, Wolff 1977), and wolves (*Canis lupus*) are good candidates for the study of dispersal (Fuller et al. 2003). Accordingly, different aspects of wolf dispersal have been reported for both North America (Gese and Mech 1991, Boyd and Pletscher 1999, Fuller et al. 2003, Mech and Boitani 2003) and northern Europe (Wabakken et al. 2001, 2006; Kojola et al. 2006), but very limited information is available for south-central Europe (Blanco and Cortés 2007), where higher human density and anthropogenic features may affect wolf dispersal to a much greater extent. In addition, because logistic and technical constraints did not allow, until recently, detailed studies of long-distance dispersal by wolves (Merrill and Mech 2000, Blanco et al. 2005), it is difficult to fully understand wolf dispersal mechanics and to predict landscape links (Fuller et al. 2003).

The advent of Global Positioning System (GPS) technology made it possible to gain new insights into wolf dispersal and connectivity among disjoint wolf populations (Kojola et al. 2006, Wabakken et al. 2006). Analyses of detailed GPS-revealed dispersal paths may provide information on how an animal perceives and moves about through the landscape (With 1994, Nams 2005). In particular, long-distance dispersal trajectories might reveal which portions of the landscape still provide connectivity between noncontiguous populations (Graves et al. 2007).

This knowledge is particularly useful in human-dominated landscapes, where spatially explicit management interven-

tions might enhance preservation and functionality of existing links for the long-term viability of metapopulations (Beier et al. 2006). For noncontiguous wolf populations across international jurisdictions, documenting long-distance dispersal is also particularly critical, because it provides evidence of their genetic and demographic connectivity, therefore supporting the need for population-based, interstate management programs (Boitani 2003, Linnell et al. 2007).

In southern Europe, long-distance dispersal by wolves has recently been inferred using noninvasive genetic data of the naturally expanding wolf population across the Italian, French, and Swiss Alps (Lucchini et al. 2002, Valière et al. 2003, Fabbri et al. 2007). Although these studies clearly indicated that wolves in the Alps originated genetically from the Apennine source population, they did not reveal dispersal trajectories or sufficient evidence to resolve the animated debate on the origin of the recolonizing wolves in France (Spagnou 2003a). Whereas wolf opponents did not rule out illegal release of captive wolves (Lucchini et al. 2002), some local experts were skeptical that wolves from the Apennines could successfully travel through the narrow and altered Ligurian Apennines to reach the Alps (Zunino 2003, quoted in Spagnou 2003b, in litteris).

By using GPS telemetry, we hereby document the first report of long-distance wolf dispersal from the northern Apennines in Italy to the western Alps in France. Although based on a single event, this case provides evidence that the transboundary wolf population in the western Alps could have originated naturally from long-distance dispersers from the Apennine source population. The wolf dispersal trajectory we report directly demonstrates that a single,

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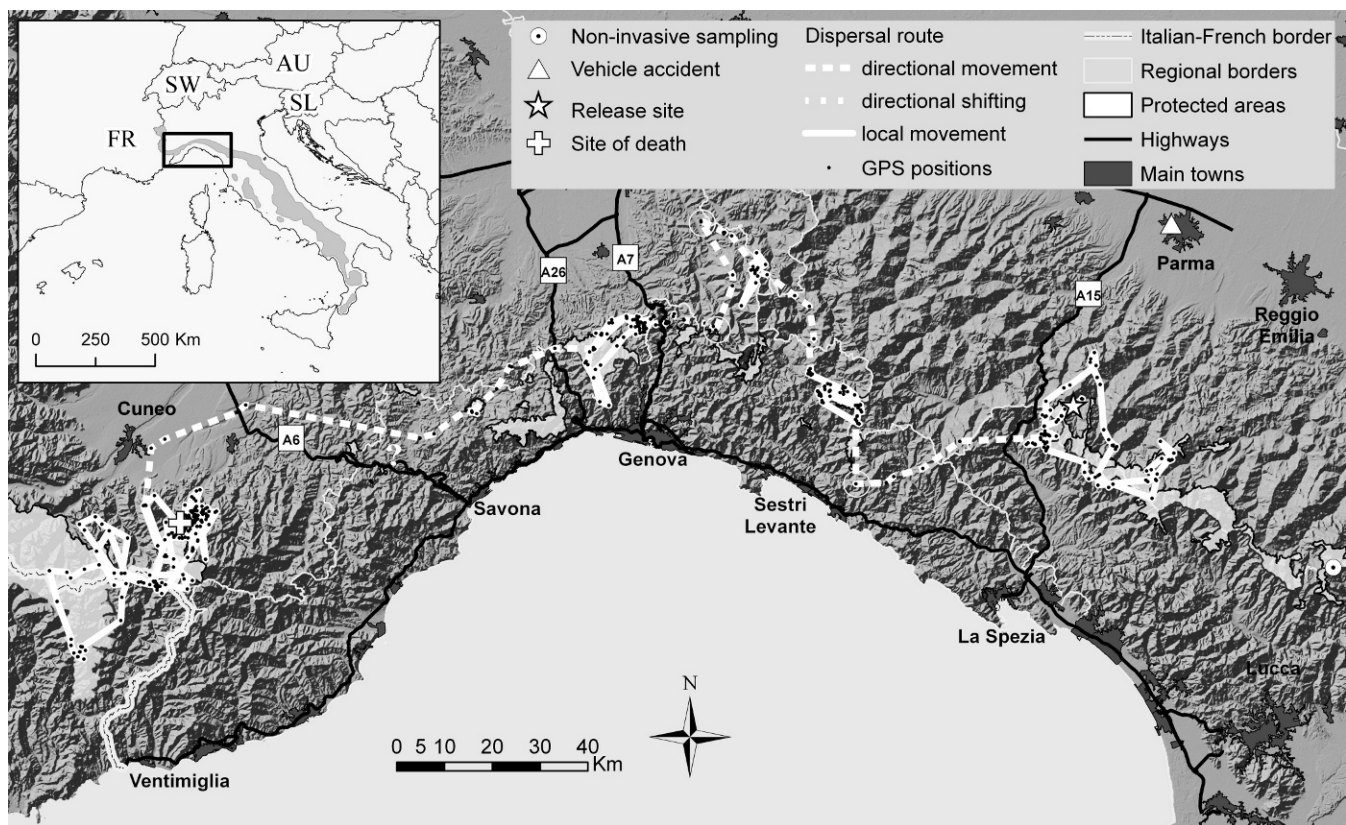


Figure 1. Global Positioning System (GPS)-estimated long-distance dispersal path of wolf pup M15, from the northern Apennines (Italy) to the western Alps across the Italian–French border (11 Mar 2004–22 Jan 2005). Only selected towns (i.e., >10,000 inhabitants) and the main protected areas close to the dispersal trajectory are shown. Open circles display sharp turning angles during directional dispersal, whereas the question mark corresponds to 4 days of missing data (22–25 Sep 2004).

narrow link still connects the 2 wolf populations across a highly heterogeneous and human-dominated landscape.

STUDY AREA

We defined the study area by the outermost locations of the dispersing wolf (Fig. 1), including the northern Apennines, in Italy, and part of the southwestern Alps across the border between Italy and France. Both areas were characterized by rugged, mountainous terrain with altitudes up to 1,978 m in the Apennines and 3,084 m in the Alps. Deciduous (mostly beech, *Fagus sylvatica*) forests covered about 51% of the Apennines, whereas the Alps featured 66% forest cover, mostly composed by conifers (*Abies alba*, *Larix decidua*) and, at lower elevations, deciduous trees (*F. sylvatica*, *Acer platanoides*, *Betula pubescens*). Wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), and red deer (*Cervus elaphus*) were locally abundant and heavily used by wolves, both in the northern Apennines (Meriggi et al. 1996) and in the Alps (Marucco 2003, Gazzola et al. 2005). Livestock, mostly free-ranging cattle, was available to wolves all year, especially in the northern Apennines. Wolf distribution in the Alpine portion of the study area was continuous and expanding (Lucchini et al. 2002, Marucco 2003, Valière et al. 2003) but it was separated from the source Apennine population by a gap of more than 200 km (Fabbri et al. 2007).

Following expansion of the wolf population in the central Apennines during the past 30 years (Boitani and Ciucci 1993), the wolf range in the northern Apennines was continuous up to about 44°40'N latitude (Ciucci et al. 2003) at the time of the study. However, it was believed to be more discontinuous along the narrow, northwesternmost portion of the Apennine chain (Meriggi et al. 2002). Snow cover usually extended from November and December to April in the Alps and from December and January through March in the northern Apennines. Human density averaged 52.8 (± 346.5 SD) and 50.1 (± 307 SD) people/km² in the Apennines and in the Alps, respectively, although its dispersion varied considerably on a local scale. Mean densities of permanent roads (highways, other paved roads, and improved unsurfaced roads passable by 2-wheel drive vehicles; Mladenoff et al. 1995) were 2.98 km/km² and 1.97 km/km² in the Apennines and in the Alps, respectively. Agriculture and other anthropogenic cover types accounted for slightly more than 50% in the Apennines, but less than 10% in the Alpine range (Falcucci et al. 2007). The Italian portion of the study area included 5 regional and several more provincial administrative units, each with their own land use and wildlife management jurisdiction, and several protected areas (1,699 km²; 14% of the study area; Fig. 1).

METHODS

On 11 March 2004, we released in the northern Apennines a 28-kg male wolf pup M15 (10 months old, age estimated by tooth eruption and wear; Gipson et al. 2000) rescued on 24 February 2004 from a vehicle accident in the outskirts of the city of Parma (Fig. 1). Immediate examination upon rescue revealed limited external and internal bleeding, and a slight limp at the front left leg (G. M. Pisani, Province of Parma, personal communication). To avoid risks of human habituation, in less than 24 hours, we moved the wolf to a small and isolated stone hut within a nearby protected area (Cento Laghi Regional Park) in the northern Apennines, as the wolf gave signs of quick recovery. We fed M15 road-kills (roe deer) and assessed its condition by observation at a distance every 1 to 2 days (M. Andreani, Cento Laghi Regional Park, personal communication). After 15 days, as the wolf was quickly recovering, we released it in a secure place nearby, located in the interstice between the territories of 2 wolf packs (Ciucci et al. 2003). Upon release, we sedated (medetomidine and ketamine, antagonized upon release with atipamezole; Kreeger et al. 2002) and fitted wolf M15 with a Televilt (Lindesberg, Sweden) GPS-Direct collar. Although the natal territory of wolf M15 was unknown, its 12-microsatellite genotype matched a known genotype (E. Randi, National Institute of Wildlife, personal communication), whose corresponding fecal sample was previously (6 Dec 2003) collected at about 80 km southeast along the northern Apennine chain (D. Pagliai, Alto Appennino Modenese Regional Park, personal communication; Fig. 1). It is thus plausible that wolf M15 was born from one of the packs in that portion of the Apennines (Ciucci et al. 2003).

We retrieved data, including location, date, time, and estimates of position quality (2D, 3D, and 3D+), from the collar through the Global System for Mobile Communications (GSM). We allowed 180 seconds for each fix attempt, and programmed the collar to acquire locations at 4-hour (until 4 May 2004) and 12-hour (after 5 May 2004) intervals. Field crews investigated clusters of GPS locations during the postrelease period, at highway crossings, and after settlement. We permanently lost GSM contact with the collar by 22 January 2005, but only by 18 February 2005 did the field crew localize the carcass of wolf M15 by homing in on the very high frequency signal. When found, the wolf had probably died ≤ 10 days before and had been entirely consumed by scavengers, making it impossible to determine the cause of death.

We projected wolf M15 locations in ArcGis 9.2, assuming inaccuracy of GPS position was negligible at the scale of our analysis (expected range: <30 m to <99 m 95% of the time for 3D and 2D positions, respectively; Dussault et al. 2001, D'Eon et al. 2002). We analyzed the overall dispersal trajectory using locations recorded at 12-hour sampling intervals ($n = 484$; 0730 hr and 1930 hr), including those subsampled, at the same time intervals, from the 4-hour sampling dataset ($n = 94$).

We defined natal dispersal as the one-way movement from the release (or presumed birth) site to an independent home

range, where wolf M15 would have presumably reproduced if it had survived (Gese and Mech 1991, Boyd and Pletscher 1999, Wabacken et al. 2006, Blanco and Cortés 2007). We quantified overall net displacement as the largest Euclidean distance covered from the release site to the furthest location along the dispersal trajectory. Differently, we quantified net dispersal distance as the largest Euclidean distance from the release site to the harmonic mean of the final home range (Kenward et al. 2002). We approximated minimum distances traveled as the sum of the Euclidean distances traveled between successive 12-hour locations. Failed GPS attempts ($n = 128$) mostly comprised single locations ($n = 110$), and only 14% included 2 successive locations. In case one location was missing, we estimated it by linear interpolation between successive locations (Ciucci et al. 1997, Stoner et al. 2007) to ensure a constant sampling interval for the entire movement trajectory for movement path analyses (see below).

To explore movement patterns during dispersal, we visually inspected discontinuities in the cumulative net displacement curve, because they reflected differences in the rate and extent of geographical displacement (Fig. 2). By sequentially demarcating patterns indicating use of the same general area (i.e., little or no increase in net displacement) from those reflecting a consistent travel from the release site (i.e., no return to previously visited areas), we thus identified 11 dispersal phases, each featuring 1 of 4 different movement patterns (Fig. 2): 1) local movements, with more or less localized spatial behavior and recurrent use of the same general area; 2) directional movements, with consistent traveling in a predominant direction; 3) directional shifting, an intermediate pattern between the previous 2, when wolf M15 gradually shifted a restricted area of activity in one direction; and 4) home range-like movements, similar to local movements but more localized, reduced in extent, and for an extended period of time. We considered the home range-like movements as an indication of settlement (Gese and Mech 1991, Mech and Boitani 2003). To better characterize the multistage pattern of dispersal (sensu Wabacken et al. 2006), we used linear, fractal, and circular metrics to describe dispersal phases.

We computed fractals by the Fractal Mean method (Nams 1996) using FRACTAL (version 4.1, <http://nsac.ca/envsci/staff/vnams/Fractal.htm>, accessed 15 Jul 2009). We used basic circular statistics (Zar 1999) to describe and test directionality of travel, both within each dispersal phase (first-order samples) and within movement patterns (i.e., directional vs. local movement phases; second-order samples). In particular, we measured angular dispersion of traveling bearings by the mean vector r , a measure of angular concentration that can vary from 0 (high angular dispersion and no mean bearing) to 1 (all bearings have the same direction), and used the Rayleigh's z to test the null hypothesis of no angular concentration. We used Moore's modification of the Rayleigh test (Zar 1999) to test the hypothesis of no angular concentration in second-order samples. In statistically comparing fractal and circular metrics among dispersal phases, we assumed they were

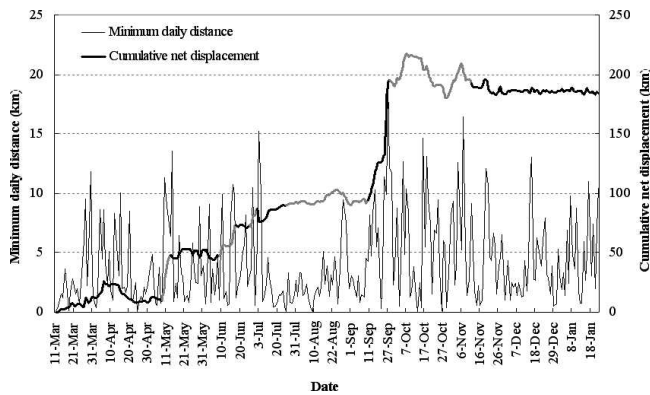


Figure 2. Minimum daily distance and cumulative net displacement traveled by wolf M15 from the release site during its Global Positioning System–revealed dispersal from the northern Apennines (Italy) to the western Alps (France and Italy; 11 Mar 2004–22 Jan 2005). We identified 11 dispersal phases on the basis of discontinuities in the cumulative net displacement curve, and they are shown by alternate black and gray sections (cf. Table 1).

independent, because wolf movements responded to different environmental and social stimuli across the different areas encountered during dispersal; however, we caution against interpreting significance levels because all movements pertain to a single wolf.

RESULTS

In 318 days since release (11 Mar 2004–22 Jan 2005), wolf M15's collar acquired 653 locations, with an acquisition rate of 76.1%. Acquisition rate did not differ between the 4-hour and the 12-hour GPS-schedules ($G_{adj,1} = 1.02$, $P = 0.31$), nor between the broadleaf (Jun–Oct) and the broadleaf-less (Nov–May) seasons ($G_{adj,1} = 2.19$, $P = 0.14$). At the 12-hour sampling, acquisition rate of GPS locations was higher in the evening (83.5%, at 1930 hr) than in the morning (72.2%, at 0700 hr; $G_{adj,1} = 9.34$, $P = 0.002$). Most locations (66.6%) were of high accuracy (3D, 3D+), and their proportion was not affected by sampling interval ($G_{adj,1} = 0.11$, $P = 0.74$) or vegetative season ($G_{adj,1} = 0.52$, $P = 0.47$). Since deployment, both measures of GPS performance did not vary with increasing battery drainage on a monthly basis (acquisition rate: $F_{1,9} = 0.08$, $P = 0.78$; proportion of 3D locations: $F_{1,9} = 0.05$, $P = 0.82$).

Following release, wolf M15 spent about 2 months roaming north, east, and southeast of the release site in an area of about 514 km², where we knew at least 3 other packs existed (Fig. 1). During this period, at least 8 ground investigations on clusters of ≥ 2 locations, partly aided by snow, provided evidence that wolf M15 was traveling alone and was feeding on roe deer, wild boar, and occasionally on livestock carcasses (M. Andreani, personal communication). Wolf M15 then abandoned this area and began traveling at a faster pace in a west–northwesterly direction along the Apennines, eventually reaching the French Alps by 2 October 2004, about 7 months after release. Wolf M15 then floated for about one month across the Italian–French border, using an area of about 694 km² in the same general locality where in 1993 the first noninvasive genetic sample

of a recolonizing wolf was collected (Valière et al. 2003). We knew a minimum of 3 wolf packs resided in that area at the time wolf M15 arrived (Wolf Alpine Group 2004). By 8 months after release, wolf M15 eventually began to restrict its movements and settled on the Italian side of the Alps for 2.5 months, carving out a home range (95% fixed kernel) of 71.8 km² in an area between 2 resident wolf packs. Since December 2004, a field crew investigated wolf M15's tracks in the snow (16 sessions, 44 km), and revealed that in 88% of these sessions, wolf M15 was associated with another wolf (F. Marucco, Piemonte Large Carnivores Project, personal communication). Noninvasive genotyping later confirmed that by 16 January 2005 wolf M15 had permanently paired with wolf F70, a yearling female from one of the resident packs (M. Schwartz, Rocky Mountain Research Station, personal communication). The same winter, wolf F70 was tracked alone from 9 February onward (F. Marucco, personal communication), probably following the death of wolf M15.

The furthest location wolf M15 reached during dispersal was on the French side of the western Alps, for a maximum net displacement of 217.3 km. Conversely, net dispersal distance was 186.8 km, considering the release site, or 239.7 km with respect to the putative natal range (Fig. 1). The net dispersal distance from the release site corresponded to a minimum distance traveled of 958 km, which, corrected by a factor of 1.3 (Musiani et al. 1998, Wabakken et al. 2006), yields an estimate of 1,245.3 km actually travelled.

Geographical displacement during dispersal was not constant over time, and discontinuities in cumulative net displacement indicated 11 sequential dispersal phases (Fig. 2). Excluding directional shifting for which data were incomplete, directional movements ($n = 4$ phases) contributed the most to net ($\bar{x} = 44.9$, $SD = 37.8$ km/phase) and daily ($\bar{x} = 8.6$, $SD = 0.6$ km/day) distance travelled, whereas local movements ($n = 5$, excluding home range–like movements), contributed less ($\bar{x} = 20.1$, $SD = 10.4$ km/phase, and $\bar{x} = 3.4$, $SD = 1.2$ km/day for net and daily displacement, respectively). Accordingly, phases featuring local movements ($n = 5$) were on average more tortuous than directional movements ($n = 4$; Fractal D: $\bar{x} = 1.52$, $SD = 0.21$, and $\bar{x} = 1.20$, $SD = 0.06$, respectively; $t_7 = -2.96$, $P = 0.021$; Table 1). During localized phases wolf M15 travelled minimum distances of 5.7–16.4 km/day, indicating that it was not stationary but moved intensively in the same general area, possibly searching for other wolves or resources. Individually considered, directional phases had a predominant traveling direction ($0.20 \leq r \leq 0.81$; $3.49 \leq \text{Rayleigh } z_{5-14} \leq 6.79$, $0.001 \leq P \leq 0.05$), whereas localized phases did not reveal any particular directionality ($0.02 \leq r \leq 0.15$; $0.00 \leq \text{Rayleigh } z_{10-112} \leq 1.16$, $P > 0.05$). Accordingly, directional phases had little angular dispersion ($r = 0.81$) and an overall bearing of 266.1°N ($SD = 37.1^\circ$ N; Moore test: $R_5 = 1.10$, $P < 0.05$), whereas, in contrast, localized phases did not display a preferred traveling bearing (Moore test: $R_6 = 0.47$, $P > 0.50$).

Wolf M15's dispersal trajectory extended through the main Apennine chain, with an overall mean bearing of

Table 1. Sequential phases of wolf M15 dispersal from the northern Apennines (Italy) to the western Alps (France) based on 484 Global Positioning System (GPS) locations acquired at 12-hour intervals (Mar 2004–Jan 2005).

Movement pattern	Dispersal phase	Date	No. GPS locations	Net displacement (km) ^a		Min. distance traveled (km) ^b					Fractal-D ^c	Directionality	
				Greatest	Day ⁻¹	Total	Daily			Mean vector		Mean bearing (°N) ^d	
							Mean	SD	Min.				Max.
Local	1	11 Mar–7 May	98	25.6	0.4	173.2	3.0	2.8	0.1	11.8	1.45	0.05	59.7
Directional	2	8–14 May	7	39.9	5.7	54.8	7.8	2.9	5.6	13.5	1.23	0.76	262.7*
Local	3	15 May–13 Jun	55	13.9	0.5	92.2	3.1	2.6	0.1	9.9	1.81	0.14	295.8
Directional	4	14–17 Jun	7	24.6	6.2	28.5	7.1	3.7	3.2	10.7	1.16	0.81	331.0**
Local	5	18–27 Jun	12	8.0	0.8	29.8	3.0	2.4	0.6	5.7	1.34	0.01	111.0
Directional	6	28 Jun–4 Jul	10	15.5	2.2	42.0	6.0	5.0	0.6	15.2	1.27	0.20	251.9
Directional shifting	7	5–26 Jul ^e	23	12.8	0.6	20.1	0.9	0.7	0.1	2.1	1.24	0.32	268.2
Local	8	27 Jul–12 Sep	74	18.4	0.4	127.0	2.6	2.1	0.1	9.5	1.34	0.06	250.4
Directional	9	12–28 Sep ^f	16	99.6	5.9	117.4	6.9	4.7	0.8	19.5	1.13	0.65	242.4***
Local	10	28 Sep–11 Nov	71	34.7	0.8	256.5	5.7	4.2	0.1	16.4	1.64	0.01	57.3
Home-range like	11	12 Nov–22 Jan	114	9.5	0.1	285.0	4.0	3.1	0.5	13.0	1.91	0.07	110.8

^a Greatest net displacement from the first location of current phase.

^b Cumulative Euclidean distances summed across successive locations.

^c By the Fractal Mean method (Nams 1996) using FRACTAL. Min. and max. scales were constrained by the average step size and one-third of total path length, respectively (With 1994), and 10 divider lengths were used to measure the length of each movement path.

^d Marked values from angular distributions different from uniform expected (Rayleigh test; * $P < 0.01$; ** $P < 0.001$; *** $P < 0.001$).

^e Data from 8–14 Jul were lost due to downloading failure.

^f Data from 22–25 Sep were lost due to downloading failure.

264.5°N, at altitudes ranging from 270 m to 2,664 m. During directional dispersal 3 sharp turning angles (phases 2 and 6; $\bar{x} = 124.2^\circ\text{N}$, $\text{SD} = 24.8^\circ\text{N}$, in absolute values) were on average greater (Watson and William test: $F_{1,36} = 14.89$, $P < 0.001$) than the overall mean of directional movements ($\bar{x} = 44.8^\circ\text{N}$, $\text{SD} = 37.6^\circ\text{N}$, $n = 40$), suggesting the wolf's attempt to redirect and maintain its traveling along the main Apennine chain as it reached lower elevations or increasingly developed areas (Fig. 1).

During dispersal, wolf M15 traveled across 2 national, 5 regional, and several provincial administrative units, and went as close as 0.8–5 km to large towns such as Cuneo and Genoa. The wolf navigated several potential barriers, including 4 fenced 4-lane highways (traffic volumes in Jul–Sep 2004 ranging 49,928–143,081 vehicles/day; AIS-CAT 2004), several main railways, and many state, provincial, and local paved roads. Wolf M15 crossed highways with apparent ease (≤ 12 –24 hr) and, as from field investigations, systematically used underpasses, which are frequent along highways in these mountainous areas. As an exception, wolf M15 clustered for 4 days at 700–1,100 m east of highway A7 before crossing it. Although we cannot exclude the presence of a carcass at the site, the juxtaposition of the highway, an unfenced 2-lane state road, a railway, and a river, all at the bottom of a steep valley flanked with concrete banks >10 m high, might have presented wolf M15 with a serious challenge, thereby delaying its movements. At the edge of the northwestern Apennines, while traveling in a southwesterly direction, wolf M15 turned northwestward before crossing highway A6, thus reaching the westernmost portion of the Po River Valley at altitudes as low as 300 m. Unfortunately, having lost GSM data during this period (22–25 Sep 2004), we cannot assess whether this change of direction might have resulted from a

failure in negotiating a more direct route to cross highway A6 (Fig. 1). However, wolf M15 crossed highway A6 further north, utilizing the 900-m-wide, riparian vegetation-rich drainage of the Pesio River running underneath the highway. By following the same drainage for an additional 11 km, wolf M15 eventually reached the densely populated outskirts of Cuneo, where it turned southward to finally reach the Alps in less than 48 hours (Fig. 1). In this heavily cultivated and developed area, wolf M15 traveled at a fast pace during the night (15–16 km/night) and rested during the day, using the thick and locally widespread corn plantations.

DISCUSSION

Being based on a rescued wolf, our study differs from other telemetry-based wolf dispersal studies (Boyd and Pletscher 1999, Kojola et al. 2006, Wabakken et al. 2006, Blanco and Cortés 2007). We cannot therefore exclude that actual dispersal distances were higher than those reported, or that the prerelease events (vehicle accident, rescue, and recovery) might have influenced to some extent wolf M15's subsequent dispersal behavior. Nevertheless, the observed natural dispersal behavior supports the idea that limited handling and no contact with humans during the brief recovery were successful in avoiding conditioning or habituation effects.

Although our results are based on a single case, they provide clear evidence that wolves can disperse through the human-dominated landscapes of the northern Apennines. Wolf M15's dispersal trajectory directly demonstrates that a functional linkage still exists between the Apennine and the Alpine wolf populations. This was previously inferred from genetic studies, based on which unidirectional and male-biased dispersal from the Apennine population could have

occurred repeatedly at a rate of 1.25–2.5 wolves/generation (Fabbri et al. 2007).

Although wolves may disperse as much as 390–1,092 km (Boyd and Pletscher 1999, Wabakken et al. 2006), wolf M15 traveled a dispersal distance higher than the average reported for wolves in the more pristine landscapes of North America (77–113 km; Gese and Mech 1991, Boyd and Pletscher 1999, Mech and Boitani 2003) and northern Europe (99 km; Kojola et al. 2006). This dispersal distance is the highest so far documented by means of telemetry in the human-dominated landscapes of southern Europe (Spain: Blanco and Cortés 2007; Italy: P. Ciucci, Sapienza University of Rome, unpublished data).

Dispersing wolves seem to maximize breeding opportunities rather than resource acquisition (Boyd et al. 1995, Wydeven et al. 1995, Mech and Boitani 2003). Therefore, they may travel long distances due to the low probability of finding a mate (Boyd and Pletscher 1999, Wabakken et al. 2006). However, not only conspecific attraction (Boyd and Pletscher 1999, Blanco and Cortés 2007), but also the rough and irregular topography of the Apennines chain north of the release site may have influenced both distance and direction of wolf M15's dispersal. Similarly to dispersing wolves in Montana, USA, which used a narrow swath along the Rocky Mountain chain where other wolves were present (Boyd et al. 1995), wolf M15's movements appeared to be funneled along the narrow stretch of the northern Apennines, confirming a previously postulated linkage effect of this tract of the Apennines between the Apennine and the Alpine wolf populations (Mech and Boitani 2003, Fabbri et al. 2007).

Wolf M15's dispersal confirms the ability of wolves to cross areas previously believed to act as barriers, such as open, agricultural, and developed areas, or other linear infrastructures (Mech et al. 1995, Merrill and Mech 2000, Fuller et al. 2003, Valière et al. 2003, Blanco et al. 2005). Elsewhere, however, highways with much lower traffic volumes (4,000 vehicles/day) act as barriers to wolf movements through direct mortality (Paquet 1993) and reduced movement rates (Alexander et al. 2005). Although we cannot infer population level responses from a single event, we believe that in the Apennines highway crossing may be facilitated by naturally occurring mitigation provided by the many under- or overpasses largely negotiable by wolves while traveling. Nevertheless, as exemplified by wolf M15's crossing of highway A7, the local juxtaposition of several linear structures may represent a more difficult obstacle, especially for dispersing wolves without prior spatial knowledge of the area (see also Blanco et al. 2005).

Management Implications

Wolf M15's dispersal conclusively demonstrates that wolves from the Apennines can travel across the altered landscape of the Ligurian Apennine chain to reach the Alps, supporting previously inferred conclusions from genetic studies on the natural recolonization of the Alps by long-distance-dispersing wolves from the Apennines (Lucchini et al. 2002, Valière et al. 2003, Fabbri et al. 2007). Because we made wolf M15's case public after its death, it was reported by most national

and local news media in France, which presented this case as proof that wolves have returned to the Alps naturally (B. Lequette, Mercantour National Park, personal communication). As a consequence, shepherds and farmers' organizations also ceased to openly support the artificial reintroduction hypothesis. Hard data from a single wolf outweighed all logical and biological inferences offered by scientists on the natural expansion of the wolf range throughout northern Italy and the Alps (Lucchini et al. 2002, Valière et al. 2003). Acceptance of the natural recolonization process implied that the wolves in the Alps are fully protected under the provision of the Habitat European Directive and should be allowed to establish a viable population. The ultimate evidence of the habitat and population continuity across the Italian–French boundary has been instrumental in prompting formal meetings of the Italian, French, and Swiss authorities to discuss a road map toward a common management plan of the Alpine wolf population.

In this perspective, the functional connectivity between the Apennine (source) and Alpine (colony) wolf populations should be maintained, at least at the estimated current rate (Fabbri et al. 2007) deemed sufficient to counteract serious bottleneck effects for the Alpine wolf population. Our results contributed to highlighting the landscape linkage across the Ligurian Apennines for its future preservation and mitigation of potential barriers.

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