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SHORT COMMUNICATION

Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf (*Canis lupus*) populations

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Abstract In the last two centuries, persecution and deforestation caused grey wolf *Canis lupus* populations in Europe to decline. Recently, their numbers started to recover although most populations still remain isolated from one another. This study presents the first documented evidence of the successful reconnection of the Dinaric-Balkan and the Alpine wolf populations via long-distance dispersal and subsequent reproduction. A young male wolf radiocollared in the Dinaric Mountains in July 2011 travelled through Slovenia and Austria to the Italian Alps, where he settled in March 2012. During the 98 days of dispersal period, the wolf has travelled a cumulative line distance of 1176 km crossing multiple anthropogenic and natural barriers, and successfully hunting wild prey until he settled 233 km straight line distance from its natal territory. Camera trapping, snow tracking and genetic evidence in the new territory confirmed pairing with a female wolf from the neighbouring Alpine population. In the following year, the pair has produced a first documented "mixed" litter between wolves from the Dinaric-Balkan and the Alpine wolf populations. This case study demonstrates the potential for the future merging of European wolf populations even in human-dominated landscapes and highlights the importance of transboundary cooperation in wolf research and management.

Keywords Grey wolf · *Canis lupus* · Long-distance dispersal · GPS collar · Population joining · Recolonization · Central Europe

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Introduction

Long-distance dispersal of grey wolves *Canis lupus* over several hundreds of kilometres has been usually reported from remote regions with low human population densities in North America and northern Europe (Fritts and Mech 1981; Fritts 1983; Merrill and Mech 2000; Wabakken et al. 2001, 2007; Kojola et al. 2009; Linnell et al. 2005). Only a few cases are well documented in human-dominated landscapes in western, central or southern Europe (Blanco and Cortes 2007; Ciucci et al. 2009; Fabbri et al. 2014; Andersen et al. 2015; Reinhardt and Kluth 2011).

Dispersal is a crucial mechanism for ensuring an adequate gene flow within a metapopulation and aids in the process of (re) colonization. After substantial reduction in range and greatly decimated numbers in previous centuries, wolf populations have started to recover throughout Europe, increasingly spreading back also into more human-dominated landscapes (Chapron et al. 2014). Based on existing data on wolf distribution, as well as a range of geographic, ecological, social and political factors, ten wolf populations are presently

recognized in Europe (Kaczensky et al. 2013). Until recently, most of these wolf populations were believed to be isolated, including Dinaric-Balkan and Alpine populations, which have been separated for over a century. Here, we report on a successful long-distance dispersal of a 2-year-old male wolf from the Dinaric-Balkan population to the Eastern Italian Alps, which resulted in the first documented "mixed" litter between the Dinaric-Balkan and the Alpine wolf population and successful recolonization of an area where wolves have been extirpated more than a century ago.

Material and methods

Study area

The study area is located in the Eastern Alps and northwestern part of Dinaric Mountains (45° 23′–47° 07′ N and 10° 49′–14° 33′ E) spanning through Slovenia, Croatia, Austria and Italy (Fig 1). The area is characterized by a mosaic of various landscape structures, including forests, agricultural land, larger cities, smaller settlements and rugged high mountains. Potential main wild prey species present include roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, chamois *Rupicapra rupicapra* and wild boar *Sus scrofa*. In addition, the area is used for livestock grazing, primarily sheep and cattle.

Data collection

A male wolf was captured in the Mt. Slavnik region in southwestern Slovenia and immobilized using standard protocols (Kusak et al. 2005). Its age was estimated based on the body size and overall appearance, tooth wear (Gipson et al. 2000), date of capture and genetic monitoring of the pack from the previous year. After examination and measurements, the wolf was fitted with a GPS-VHF collar (Vectronic Aerospace, 582 g). The collar has been programmed to attempt a GPS position every 3 h and 10 min. Dispersal distance was calculated as the cumulative distance between successive GPS fixes and as straight line distance between natal and new territory. Home range sizes were calculated based on the 100 % minimum convex polygon of pre- and post-dispersal GPS locations. Snow tracking and GPS location cluster analyses were used to locate prey in order to collect scat samples for non-invasive genetic identification and other evidence of wolf presence. For photo trapping, IR-PLUS BF HD cameras were used. Genetic analyses were done at I.S.P.R.A., Carnivore Genetics (Italy), and at Biotechnical Faculty, University of Ljubljana (Slovenia), using routine protocols (Majić Skrbinšek 2013).

As the wolf moved, a network of wolf experts involved in monitoring of the dispersal expanded and communication among the experts and local wildlife managers was carried out mainly via a custom-created discussion group

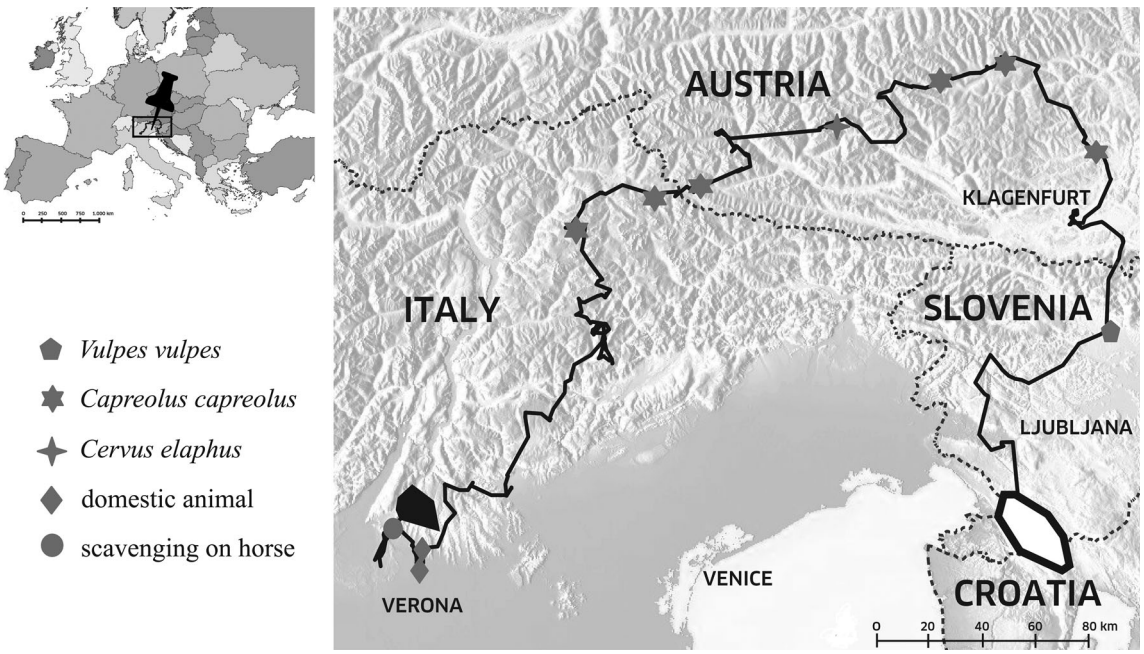

Fig 1 Long-distance dispersal of male grey wolf Slavc from a transboundary pack in the Dinaric Mountains through Slovenia and Austria to the Eastern Alps in Italy between 20th December 2011 and 26th March 2012. The natal territory in the Dinaric Mountains is marked in *white* (442 km^2 from 17th July to 19th December 2011) and the new territory in the Italian Alps in *black* (150 km^2 from 27th March 2012 to 27th August 2012). The cumulative distance of the dispersal route is 1176 km, and the straight line distance between the natal and new territory is 233 km. See legend for detected predation/scavenging event locations along the dispersal route

(Google Groups). Media clips reporting on the dispersal were collected and regular updates shared with the interested publics.

Results

A non-breeding male (nicknamed "Slavc") estimated to be 2 years old was captured in Slovenia on 17th July 2011. The wolf was a member of the transboundary Slovenian-Croatian pack "Slavnik", the most western pack of the Dinaric-Balkan population (Potočnik et al. 2014). We monitored Slavc's movements for 407 days, until the drop-off mechanism was activated on 27th August 2012. GPS fix success rates before, during and after dispersal were 90.1, 86.2 and 85.3 %, respectively, and we obtained a total of 2245 GPS locations. During the first 5 months of monitoring (17th July until 19th December 2011), the wolf stayed within the 442-km^2 birth pack's home range.

On 20th December 2011, the wolf started to disperse. During the following days of dispersal, Slavc crossed Slovenia, large part of Austria and part of the Italian Alps (Fig 1). It crossed anthropogenic and natural barriers, such as major highways, railways, urbanized and cultivated areas, river dams, large rivers and snow-covered mountain ridges (Table 1). We inspected 15 GPS clusters and found wolf scavenging on a horse carcass and ten prey remains, which consisted of one red fox, six roe deer, one red deer calf, one domestic sheep and one goat (Fig. 1). Although the wolf was moving through landscapes with high human densities and many livestock pastures and deer farms, we obtained only one report of a possible wolf sighting and two reports of domestic animals killed during the entire dispersal phase. Dispersal was completed on 26th March 2012, when Slavc reached the Lessinia Regional Park in Italy. The cumulative line distance between locations covered during the 98-day dispersal period was 1176 km.

In Lessinia, Slavc joined a solitary female wolf (nicknamed "Julia") originating from the Alpine population. During the 5 months of monitoring after the settling down (27th March–27th August 2012), its home range size measured 150 km^2. On 12th August 2012, a dead (poisoned) female was found in the same area. However, photographic material and genetic analysis showed that it was not paired female Julia but another young female originating from the Alpine population (Calderola, pers. comm.). In 2013, the first wolf reproduction in the area was documented with camera trapping, showing two adult wolves and two pups. In the following winter, presence of four wolves was confirmed with snow tracking. In summer of 2014, seven new pups were recorded with camera trap and by the end of the same year, at least 11 animals were observed.

In total, 87 popular articles were published in national and international media about the case of Slavc's dispersal. At the end of the dispersal, 39 experts were involved in the online discussion group and 117 messages were exchanged.

Discussion

Genetic sampling is allowing us to increasingly improve documenting long-distance dispersals through human-dominated landscapes (e.g. Lucchini et al. 2002; Andersen et al. 2015; Valiere et al. 2003; Fabbri et al. 2014) throughout wolves' range in Europe; however, records of breeding between wolves originating from different populations are rare. In recent years, wolves of the Alpine, Balkan-Dinaric and East European descendent have been documented in the Alps (Lapini et al. 2010; Fabbri et al. 2007; Fabbri et al. 2014), suggesting that this region may become a melting pot for wolves of different origins (Marucco 2011).

The long-distance dispersal (1176 km) and subsequent successful reproduction of a male wolf from Dinaric Mountains with a female from the Alps is the first documented breeding between the Dinaric-Balkan and Alpine wolf populations and, according to the historic data (Garbini 1904; Benetti 2003), the first record of a wolf pack in Lessinia in the last 130 years. The case underlines that although most European wolf populations are nowadays isolated, long-distance dispersal ability will likely result in merging of several populations in the near future. If recovery trends will continue at present rate, this might enable formation of a pan-European wolf metapopulation with regular gene flow among subpopulations, which would present a crucial step towards the long-term conservation of the species. A powerful tool to detect long-distance dispersal is non-invasive genetic sampling, but samples along the dispersal routes are rare. GPS telemetry, on the other hand, allows us to understand how wolves navigate through the landscape. The cumulative travel distance of rescued wolf collared by Ciucci et al. (2009) from northern Apennines in Italy to the western Alps in France was at least 958 km and the wolf crossed several highways and travelled through agricultural areas. The presented dispersal of Slavc is another clear example illustrating that few structures or landscape features could be considered dispersal barriers for wolves. Wolves in human-dominated landscapes seem to quickly learn how to use human infrastructure for crossing of linear barriers (rivers, motorways…) like bridges (Blanco et al. 2007), over- and underpasses, tunnels and viaducts. Such structures were used by Slavc on at least 13 occasions during his journey. On the other hand, Slavc's birth pack had a heavy traffic volume fenced-in motorway SI A1 running through the part of its territory and was crossing it regularly through all possible means (viaduct, under- and overpasses (bridges, greenpasses)). This might have given Slavc the experience needed to be able to cross various linear barriers he encountered.

Table 1 Summary of major crossing events of a male wolf "Slavc" during the dispersal period through Slovenia (SI), Austria (AUT) and Italy (IT)

Date	Structure	Detail	Country	Type of traversing
19/12/2011	HW	A1 (Ljubljana-Koper)	SI	UP
19/12/2011	HW	A3 (Divača-Trieste)	SI	UP
20–21/12/2011	HW	H4 (Razdrto-Ajdovščina)[a]	SI	UP/VI
25/12/2012	*RI*	Sava	SI	SW
25–28/12/2012	HW	A2 (Ljubljana-Jesenice)[b]	SI	UP
29/12/2011	*MP*	Jezersko	SI/AUT	CR
01/01/2012	*RI*	Drava	AUT	SW[d]
04/01/2012	HW	A2 (Graz-Klagenfurt)	AUT	UP/OP
09/01/2012	*RI*	Mur	AUT	BR
14/01/2012	*RI*	Mur	AUT	BR
16/01/2012	SA	SR Katschberg	AUT	CR
17/01/2012	HW	A10 (Villach-Salzburg)	AUT	TU
17/01/2012	*MP*	Poella[c]	AUT	CR
22/01/2012	*RI*	Drava	AUT	SW
27/01/2012	*RI*	Isel	AUT	SW
4–6/02/2012	SA	SA Sextner	IT	CR
7–8/02/2012	SA	SA Kronplatz	IT	CR
9–14/02/2012	SA	SA Alta Badia and Arabba	IT	CR
15/02/2012	SA	SA Falcade	IT	CR
03/03/2012	HW	A31 (Vicencia-Rocchette)	IT	UP/OP

Natural barriers are marked in italics (MP—mountain pass; RI—larger river) and anthropogenic barriers in plain script (HW—highway). Means of crossing these barriers were via an underpass (UP), an overpass (OP), a viaduct (VI), or a tunnel (TU) for highways and by swimming (SW) or crossing over a bridge (BR) for the large rivers. In winter, the wolf also crossed (CR) active and very popular ski areas (SA)

[a] Crossed at least three times

[b] Crossed at least five times

[c] In extreme winter conditions 2600 m a.s.l., $T<-15$ °C, average snow depth 1 m, up to 6-m-deep snowdrifts

[d] Wide 280 m where swimming

Monitoring Slavc's dispersal enabled collaboration among wolf researchers in Slovenia, Austria and Italy and improved networking among institutions of the involved countries. Good communication between management/research teams from the three countries and combining data from GPS telemetry with field inspections, camera trapping, genetic analysis, prey inspections and snow tracking over international borders allowed for an extremely detailed documentation of the wolf dispersal, its predatory behaviour, pairing with another wolf and eventual successful reproduction. At the same time, detailed transboundary monitoring provided ample opportunities to communicate the wolves' ability to travel rather unnoticed through human-dominated landscapes. It is crucial that species like wolves are managed as biological units and that demographic viability is achievable over larger areas (Linnell et al. 2008, Linnell and Boitani 2012, Boitani et al. 2015). Therefore adapting administrative structures is one of the key challenges transboundary management is facing (Linnell and Boitani 2012). The public and the media were well informed about the movements of Slavc (with some time lag and spatial imprecision to prevent potential poaching attempts) and the case received considerable public interest. This approach was relatively novel, since previous long-distance dispersals were made public with great delay (e.g. Ciucci et al. 2009). Important to note is that media coverage of Slavc's dispersal was received mostly positive and probably helped to improve the initial acceptance of new predator in the area.

During dispersal, the wolf persisted mainly on natural prey and although he was coming from a pack that regularly killed sheep on poorly protected pastures, Slavc mostly avoided killing the livestock, despite passing through some of the areas with abundant and unprotected livestock. However, after a bigger pack was established in 2014, livestock depredations events started to occur, causing local stakeholders to exert pressure on the authorities (Calderola, pers. comm.). Thus, despite initial positive response to the wolf recolonization, new challenges now arise for managers and special care needs to be taken when communicating with local stakeholders, especially farmers, who experience losses and are thus compelled to set the tone and steer the debate of how predators are perceived in this "new" environment.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All capture and handling methods were approved by the Slovenian Ministry of the Environment and Spatial Planning (Permit no. 35601-145/2007-6).

Conflict of interests The authors declare they have no competing interests.

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