Short communication

Beyond home: Preliminary data on wolf extraterritorial forays and dispersal in Central Italy

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ABSTRACT

Extraterritorial forays in wolves (*Canis lupus*) have rarely been documented, especially in human-modified landscapes of southern and central Europe. Integrating information on extraterritorial forays is currently enhanced by Global Positioning System (GPS) telemetry and contributes to our knowledge of the spatial dynamics of wolf populations. We hereby report GPS-revealed extraterritorial forays performed by 4 wolves in 3 packs in the Abruzzo, Lazio and Molise National Park (central Apennines, Italy, 2009–2010). Wolves engaged in extraterritorial forays almost exclusively during fall and winter, when they occurred on average every 22 days, for relatively brief periods (i.e., ≤4 days) and short distances (i.e., mean minimum travelled distance of 13.3 ± 7.2 SD km). Three extraterritorial forays were later revealed to be pre-dispersal movements, featuring longer duration and higher travelled distances than other extraterritorial forays and occurring 33–17 days prior to dispersal. We also anecdotally report two cases of dispersal, one involving an adult female that travelled 41.2 km to establish a new territory adjacent to her natal home range, and the other involving a yearling male that travelled a minimum of 422.2 km to the adjacent Majella National Park.

An increasing number of studies have been recently carried out on space use patterns by wolves living in the human-modified environments of Europe (Blanco and Cortés, 2007; Ciucci et al., 2009; Kojola et al., 2009; Llaneza et al., 2012; Mattisson et al., 2013; Mancinelli et al., 2018). Nevertheless, extraterritorial forays by wolves have rarely been addressed in these environmental contexts (Blanco and Cortés, 2007; Kojola et al., 2016). Therefore, most of the available information on extraterritorial movements by wolves refer to the more pristine ecosystems of North America (e.g., Fritts and Mech, 1981; van Ballenberghe, 1983; Messier, 1985; Merrill and David Mech, 2000). Extraterritorial forays have been defined as occasional movements beyond the home range (Bekoff, 1977). In wolves, they may be exploratory in nature and motivated by the need to locate profitable food resources (Fritts and Mech, 1981; Messier, 1985; Ballard et al., 1997; Frame et al., 2004), or to search for a mate as a prelude to dispersal (i.e., pre-dispersal movements; Fritts and Mech, 1981; van Ballenberghe, 1983; Messier, 1985; Merrill and David Mech, 2000).

By using GPS telemetry, and complementing our previous assessment of home range behaviour by wolves in the Abruzzo, Lazio and Molise National Park (PNALM, central Apennines, Italy; Mancinelli et al., 2018), we hereby report for the same wolf population beyond-the-home range movements, including extraterritorial forays, pre-dispersal and dispersal movements. To our knowledge, this is the first report of extraterritorial forays by wolves in Italy revealed by GPS-telemetry.

From 2007 to 2010, we live-captured 11 wolves and equipped them with GPS collars (Televilt-Tellus, Followit AB, Lindesberg, Sweden; and Vectronic Pro Light-1, Vectronic Aerospace GmbH, Berlin, Germany), as described in Mancinelli et al. (2018). Captured wolves were sexed, weighed, and classified as pups, yearlings, or adults based on tooth eruption and wear patterns (Gipson et al., 2000). Although short bursts of intensive GPS relocation rates (i.e., one location every 0.5–1 h) were scheduled for 10 days each month from January through April, we subsequently subsampled these data to obtain a comparable acquisition rate (i.e., 1 location/3 h) throughout the year. During winter, we used intensive snow-tracking to assess pack affiliation of GPS-collared wolves, classifying wolves as resident pack members if detected in groups of ≥2 wolves, or as floaters (i.e., lone wolves that wander around the population and frequent areas along the interstices among territories; Mech and Boitani, 2003) if consistently tracked alone during the study period. We also confirmed *a posteriori* affiliation of collared wolves using information derived from their GPS locations,

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with resident pack members sharing with other wolves the same exclusive area for ≥1 season, and floaters using larger areas across multiple wolf territories (e.g., Gehrt et al., 2009; Hinton et al., 2016).

To detect movements performed by resident wolves beyond the home range (i.e., extraterritorial forays, pre-dispersal, and dispersal movements), we first estimated annual home ranges of wolf packs using all available locations by means of 95% Brownian Bridge Movement Models (BBMMs; Horne et al., 2007). Differently from more traditional home range estimators (e.g., classical kernels), the BBMM avoids the assumption of independence among GPS locations by explicitly incorporating the time lag between them to estimate home ranges (Horne et al., 2007; Kittle et al., 2015). To apply BBMMs, we estimated the Brownian motion variance by means of the R function *liker* (*adehabitatHR* R package; Calenge, 2006) and set location imprecision at 20 m, as 93.4% of our GPS locations were 3-dimensional (i.e., with an expected error <20 m; Di Orio et al., 2003). To ease comparison with other studies, we also provide estimates of annual home ranges based on the 100% Minimum Convex Polygon (MCP). Because not all pack members were tracked for up to 12 months a year and based on the relation between the cumulative proportion of annual home range size and the number of months included in the sampling period (Mattisson et al., 2013; Mancinelli et al., 2018), we considered a sampling period of ≥7 months sufficient to accurately delineate annual home ranges.

Once we defined annual home ranges for each instrumented wolf pack, we visually inspected GPS trajectories extending beyond the 95% isopleth of their corresponding annual home range and confirmed these as extraterritorial forays if they: (a) were delineated by a movement trajectory comprising ≥3 successive locations, excluding trajectories comprising missing positions, and (b) traversed an area that was visited only in that occasion throughout the sampling period (i.e., ≥7 months). Seasonality of extraterritorial forays was assessed according to summer (May–Sep), fall (Oct–Dec), and winter (Jan–Apr; Mancinelli et al., 2018). We characterized extraterritorial forays in terms of: (*i*) duration, including the first and last locations of the corresponding trajectory within the home range; (*ii*) net displacement (i.e., the straight-line distance between the arithmetic center of the home range and the farthest location reached); (*iii*) minimum distance traveled (i.e., the sum of the Euclidean distances travelled between successive locations, including the first and last locations of the trajectory within the home range). We retrospectively defined pre-dispersal movements as those extraterritorial forays that preceded dispersal movements, and dispersal as those movements that brought wolves permanently out of their natal home range. We used net squared displacement curves (NSD; Turchin, 1998; Börger and Fryxell, 2012) to describe movement patterns during dispersal, and we estimated net dispersal distance as the linear distance from the arithmetic center of the natal home range to that of the newly established home range or the farthest location reached while dispersing (Maehr et al., 2002; Blanco and Cortés, 2007).

Sufficient data to estimate annual home ranges of resident wolves were available for 4 individuals belonging to 3 packs. When first captured in May 2009, adult female F24 (2–3 years old) was a member of the Villa pack, where it remained for 7.9 months before dispersing and establishing a new pack in January 2010 (see below). Adult female F25 (2–3 years old) was tracked for 7.5 months (October 2009–May 2010), during which it always remained a member of the Orsara pack. Adult female F23 (3–4 years old) was a floater when first captured, but established a new pack, i.e., Canneto pack, with adult male M26 (2–3 years old) in October 2009. The two wolves were tracked for 8.5 and 10.1 months, respectively, and reproduced in summer 2010. Yearling male M28 was a member of the Collelongo pack, where it remained 2.1 months before

starting its dispersal in October 2010 (see below). We detected a total of 21 extraterritorial forays, including 3 pre-dispersal movements (Table S1). On average, wolves engaged in extraterritorial forays every 22 days (range: 2–92 days) and almost exclusively during winter (44%, n = 13) and fall (50%, n = 10; Fig. 1). Extraterritorial movements lasted from 9 h to slightly less than 4 days, averaging a minimum travelled distance of 13.3 (±7.2 SD) km, or a net displacement of 10.3 (±1.9 SD) km. In two of the 11 extraterritorial forays detected for the Canneto pack, the two collared wolves were found to travel together during the entire movements, with a mean distance between their simultaneous (i.e., ±2 min) GPS locations of 11.7 (±18.1 SD) m. With the exclusion of wolf F24, whose annual home range did not overlap the home ranges of the other GPS-tracked wolves, 6 extraterritorial forays partially intersected the home ranges of adjacent packs. Specifically, 3 extraterritorial movements of wolf F25 overlapped the Canneto pack, whereas wolf F23 and M26 performed 2 and 1 extraterritorial movements, respectively, within the home range of the Orsara pack.

Female F24's dispersal was preceded by 2 pre-dispersal movements (mean travelled distance: 44.6 ± 10.8 SD km; net displacement: 13.5 ± 0.8 SD km) performed 33 and 17 days before dispersal and lasting 2.8 and 1.4 days, respectively. During actual dispersal, female F24 travelled for a minimum of 41.2 km in less than 2 days, during which she did not venture very far from her natal home range (Figs. 1, 2a), establishing a new home range, after pair-bonding, along the eastern edge of the natal one (Fig. 1). Although it was not possible to estimate the annual home range of the Collelongo pack, M28 clearly entered one pre-dispersal movement, 22 days before actual dispersal, due to its length and extensive overlapping with the trajectory of its subsequent dispersal. M28's pre-dispersal lasted 6 days, during which the wolf travelled a minimum of 147.1 km (net displacement of 44.6 km). During dispersal, wolf M28 travelled for a minimum of 422.2 km in the successive 41 days before the collar failed, corresponding to a net distance of 51.3 km (Fig. 1). During this period, wolf M28 first travelled a minimum of 45.8 km in less than one day into the Majella National Park (MNP), subsequently restricting its movements in the southern portion of the park for the successive 24 days; then, M28 resumed travelling and roamed at about 20 km southeast of the MNP where it spent the successive 15 days, prior to collar failure (Figs. 1, 2b).

The extraterritorial movements that we report refer to a relatively high and saturated wolf population inside a protected area and, to our knowledge, are the first to be documented in southern Europe by means of GPS telemetry. Some extraterritorial forays we detected occurred within the territories of neighbouring packs, even though we do not know if such movements were followed by any interaction among different packs' members. As other non-GPS-tracked packs were present in the PNALM during the study period, the occurrence of temporary territorial trespassing by wolves in this population is likely to be higher. A certain level of spatial and/or temporal overlap among wolves belonging to adjacent territories is a common feature in well-established wolf populations (Mech and Boitani, 2003). Our results are in line with this observation, given the high density of the PNALM wolf population and its tight territorial mosaic (Mancinelli et al., 2018). Unfortunately, genotypes of all GPS-collared wolves and their parental relationships are not available to better understand the social context of their movements beyond the home range.

Extraterritorial forays by wolves in the PNALM occurred quite frequently, but only during fall and winter. Extraterritorial forays by wolves in fall and winter may be related to seasonal decline in prey accessibility and the need to reach out profitable food sources (Fritts and Mech, 1981; van Ballenberghe, 1983; Messier, 1985). For example, wolves in Quebec periodically visited deer wintering areas outside their traditional pack territories in periods of low
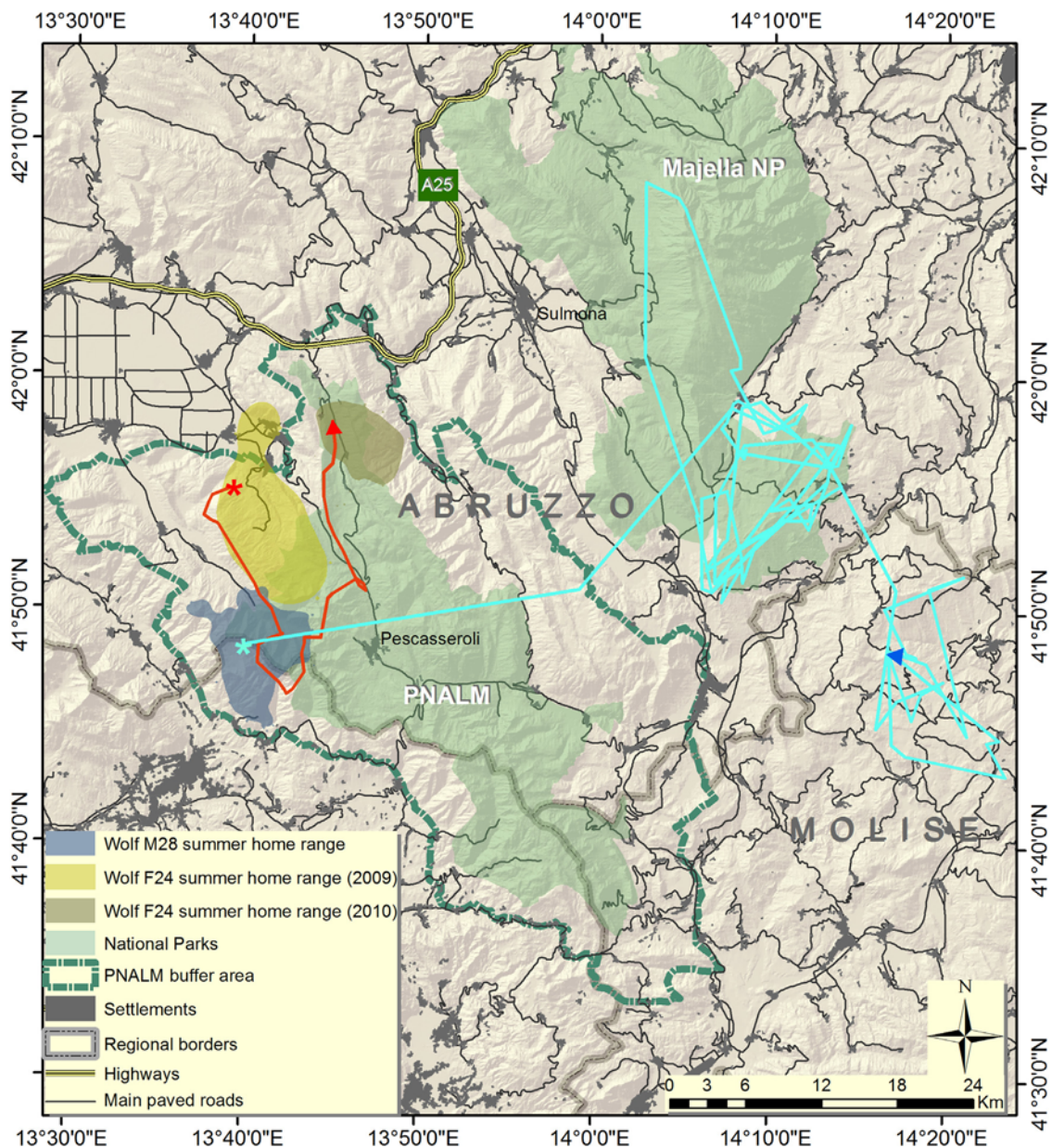
Fig. 1. Dispersal trajectories of two GPS-collared wolves in the Abruzzo, Lazio and Molise National Park, central Apennines, Italy, 2009–2010. Red line: wolf F24 (13–15 Jan 2010); blue line: wolf M28 (22 Oct–2 Dec 2010). Asterisks denote last locations in natal home ranges and arrows the first location in the newly established home range (F24), or the last location recorded (M28) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

moose density (Messier, 1985), a pattern that seems to be recurrent where wolves rely on migratory ungulates. Given the small distance travelled and the limited duration of the extraterritorial forays we detected, we doubt this was the case in our study area, even though we cannot exclude the occasional attraction of large ungulate carcasses. Free ranging cattle and horses were frequent in our study area also during the winter months, and large domestic stock that died from several causes were generally abandoned by farmers, providing an important food source to wolves (P. Ciucci, pers. comm.). Nevertheless, we believe that most of the extraterritorial forays we documented were likely related to the increase in social interactions accompanying the onset of the mating period (Messier, 1985; Fuller, 1989). Indeed, some of the extraterritorial forays we detected were pre-dispersal movements, during which territory vacancy could have been assessed by wolves before leaving the natal home range (Messier and Barrette, 1982). This could represent a frequent behavior by resident wolves living in high-

density wolf populations such as ours (e.g., van Ballenberghe, 1983; Blanco and Cortés, 2007).

Even if our sample size is clearly too small to make any inference on the mechanisms underlying the seasonal occurrence of extraterritorial forays in the PNALM wolf population, the low frequency of extraterritorial forays we detected during summer may reflect the tendency of wolves to mitigate disturbance and risk associated to human presence and activity, which are at their highest during this period of the year. Indeed, extraterritorial forays may increase mortality risk due to anthropogenic causes (Young and Monfort, 2009). This observation may be supported by the fact that, during summer, wolves in the PNALM strongly avoided anthropogenic features (i.e., paved roads and settlements; S. Mancinelli, pers. comm.). However, the paucity of extraterritorial forays reported from other high-density wolf populations in the human-modified landscapes of southern Europe does not allow comparison across wolf populations and ecological conditions, and further research is necessary
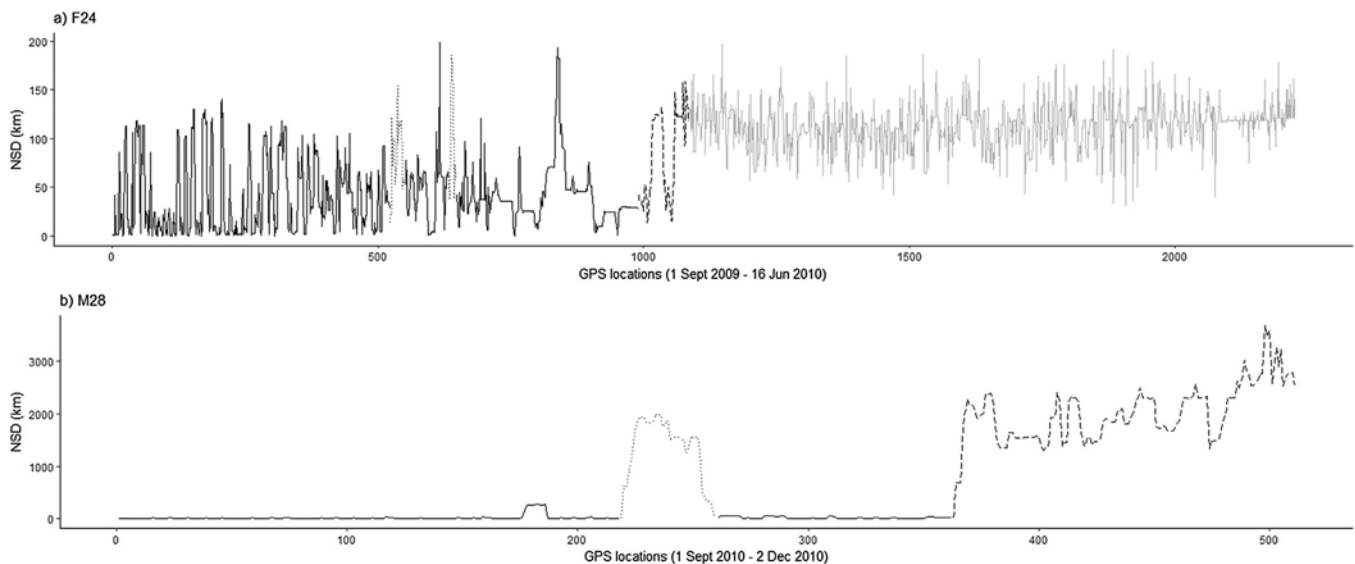
Fig. 2. Net squared displacement (NSD) curves showing, in chronological order, home-range like (solid black line), pre-dispersal (dotted line), dispersal (dashed lines) and post-dispersal (gray line; F24 only) movement patterns of two GPS-collared wolves in the Abruzzo Lazio and Molise National Park (central Italy). Note that Y-axis scale differs between panels.

to better understand occurrence of this spatial behaviour, its ecological drivers, and possible anthropogenic effects.

It is also noteworthy that the extraterritorial movements we detected in the PNALM wolf population were of relatively short length and duration compared to elsewhere (e.g., >400 km; Merrill and David Mech, 2000). Higher temporal and spatial resolution of GPS data, coupled with more accurate home range estimators, likely enhance our capabilities to detect unusual or infrequent movements outside the annual home range, especially if compared to traditional VHF telemetry and empirical home range estimators as the MCP. The higher temporal and spatial resolution of GPS data does in fact enhance detection of relatively brief extraterritorial forays by wolves, which likely went undetected in previous VHF-telemetry based studies that adopted a sparser sampling (e.g., 1–4 fix per week; Messier, 1985; Ballard et al., 1997; Merrill and David Mech, 2000). Accordingly, the extraterritorial movements we report are not necessarily comparable to those previously reported for wolves elsewhere by means of VHF and empirical home range estimators (Fritts and Mech, 1981; van Ballenberghe, 1983; Messier, 1985). It is also likely that, by means of GPS telemetry, these movements will be increasingly reported in the future; their further study, especially if associated to their causative factors, may contribute to our deeper understanding of the spatial dynamics of wolf populations.

Conversely to extraterritorial forays, wolf dispersal has been comprehensively studied throughout the species' range, even though reports from southern Europe are still very scarce (Blanco and Cortés, 2007; Ciucci et al., 2009). Although anecdotal, the two dispersal cases we report comply with two known dispersal strategies: a short-distance dispersal (wolf F24) combined with the establishment of a new wolf pack territory adjacent to the natal one (i.e., 'budding'; Mech and Boitani, 2003), believed to be rather common in saturated wolf populations, and a long-distance dispersal (wolf M28) through which dispersing wolves may seek affiliative interactions at a wider scale across the landscape (Gese and Mech, 1991; Wydeven et al., 1998; Wabakken et al., 2007; Kojola et al., 2009). In line with accumulating evidence across Europe (e.g., Blanco and Cortés, 2007; Ciucci et al., 2009; Gula et al., 2009; Kojola et al., 2009), wolf M28's dispersal trajectory also reinforces the notion that functional connectivity between wolf populations do occur in human-modified environments.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.mambio.2018.08.003.

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