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LETTER

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Military training areas facilitate the recolonization of wolves in Germany

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Abstract

Wolves (*Canis lupus*) are currently showing a remarkable comeback in the highly fragmented cultural landscapes of Germany. We here show that wolf numbers increased exponentially between 2000 and 2015 with an annual increase of about 36%. We demonstrate that the first territories in each newly colonized region were established over long distances from the nearest known reproducing pack on active military training areas (MTAs). We show that MTAs, rather than protected areas, served as stepping-stones for the recolonization of Germany facilitating subsequent spreading of wolf territories in the surrounding landscape. We did not find any significant difference between MTAs and protected areas with regard to habitat. One possible reason for the importance of MTAs may be their lower anthropogenic mortality rates compared to protected and other areas. To our knowledge, this is the first documented case where MTAs facilitate the recolonization of an endangered species across large areas.

KEYWORDS

Canis lupus, large carnivores, population growth, protected areas, recolonization

1 | INTRODUCTION

After their all-time low in the 1960s (Boitani, 2003), wolves (*Canis lupus* L.) currently show a remarkable return in central and western Europe (Chapron et al., 2014). The most important reason fostering the recovery of large carnivores in Europe was changes in legislation improving their protection status that were put into place in the 1980s and 1990s (Bern Convention and the Habitat directive). At the same time, ungulate populations have been increasing in many parts of Europe (Boitani & Ciucci, 2009; Linnell & Zachos, 2010) and public attitudes toward wildlife conservation, including large carnivores, have shifted to the positive, providing favorable conditions for their return (Boitani & Ciucci, 2009).

This is also true for Germany where wolves were eradicated in the 19th century. In the German Democratic Republic, state policy prevented any resettlement of the wolf; while in the Federal Republic of Germany, wolves had been strictly protected since 1980, albeit absent. Only after the German reunification in 1990, the wolf became strictly protected throughout the country (Reinhardt & Kluth, 2007; Reinhardt, Kluth, Nowak, & Mysłajek, 2013). In consequence, wolves emigrating from Poland have recolonized Germany since the late 1990s (Reinhardt & Kluth, 2007; Reinhardt et al., 2013). The

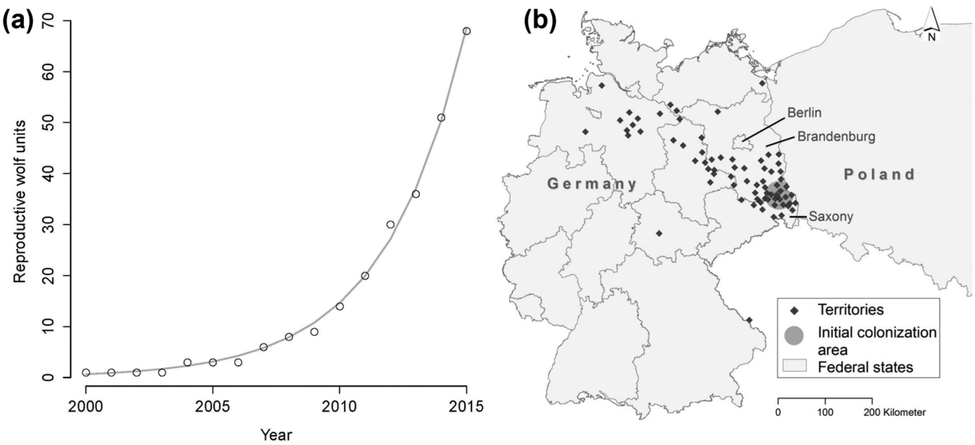

FIGURE 1 (a) Exponential increase of reproductive wolf units in Germany from 2000 to 2015. (b) Distribution of all wolf territories documented in Germany in 2015 (data from DBBW, 2017)

first colonization area was in the Saxony-Brandenburg region (Figure 1b) close to the Polish border where, in 2000, the first reproduction of wild wolves was documented (Kluth, Ansorge, & Gruschwitz, 2002). Since then, a rapid recolonization in Germany led to a population of 47 wolf packs and 21 pairs in 2015/2016 (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf [DBBW], 2017). Wolves spread across the country with wolf territories in 7 out of 16 federal states in 2015 (Figure 1b). Although wolves are known to be adaptive in respect to habitat requirements (Boitani, 2000), they prefer sites where the degree of human disturbances is low, especially when rearing pups (Kaartinen, Luoto, & Kojola, 2010; Llaneza, García, Palacios, Sazatornil, & López-Bao, 2016; Sazatornil et al. 2016). This raises the question how the remarkably fast population recovery in a densely populated and highly fragmented country like Germany was possible. How important, for example, were protected areas (PAs), for the recolonization process? Interestingly, the first wolf territory occurred on an active military training area (MTA) (Kluth et al., 2002). Subsequently, wolf territories have been established on different MTAs but also on PAs, and other lands (Reinhardt & Kluth, 2007; Bundesministerium für Umwelt Naturschutz Bau und Reaktorsicherheit [BMUB], 2015). We quantified the population growth, analyzed mortality events, and reconstructed the spatial patterns of wolf recolonization based on existing data from official monitoring reports and a public database. We focused, in particular, on the role of PAs and MTAs for the recovery of wolves in Germany. While MTAs are known to be valuable areas for nature conservation (Aycrigg, Belote, Dietz, Aplet, & Fischer, 2015; Lindenmayer et al., 2016; Zentelis & Lindenmayer 2015; Zentelis, Lindenmayer, Roberts, & Dovers, 2017), their role in facilitating recolonization processes of large mammals in human dominated landscapes has not been explored to date. We expected MTAs and PAs, to be important areas for the recovery of wolves in Germany.

2 | METHODS

We estimated the population growth of wolves in Germany since their return in 2000 until 2015 by using the number of reproductive units (packs and pairs). These data are annually collected according to the rigorous German national monitoring standards for large carnivores (Reinhardt et al., 2015) and are yearly published in official reports (Reinhardt et al., 2013; DBBW, 2017). We then fitted an exponential growth model to the data and calculated the annual population growth. For all statistical analyses, we used the programming language R (R Core Team 2016). For analyzing the spatial spread, we referred to established wolf territories (of packs, pairs, or single resident wolves) that were identified and defined by criteria of the national monitoring standards (Reinhardt et al., 2015). The location types of the territories were classified as "protected area," "military training area," or "other" (for details, see the Supporting Information). We used the federal states of Germany as spatial scale of analysis, because wolf monitoring is conducted on a state-by-state basis. We then identified where the first (up to five) territories were located in each federal state after the initial colonization happened in the Saxony-Brandenburg border region (Supplemental Figure 1). In order to exclude short-term occurrences, we only included territories that were occupied for at least three consecutive years and still existed when analyzing the data in 2017 (long-term territories).

To analyze how far wolves moved to establish new territories, we calculated the minimum dispersal distance for all wolf territories established between 2000 and 2015 by measuring the distance between the focal territory and the next known potential source territory in Germany (i.e., the next pack with confirmed reproduction in the previous year). Using the minimum dispersal distance, we ignored that territory founders might have immigrated from Poland or other European countries. However, comparing our distribution data to Poland

(Nowak & Mysłajek 2016) or other countries, the next possible source territory outside Germany was usually farther away for newly established wolf territories than the next source territory within Germany. Our dispersal distances are therefore conservative. We log-transformed the dispersal data and performed linear mixed models with federal state as random effect to test whether the minimum dispersal distance differed between territories established on MTAs, PAs, or other areas. In addition, we mapped the dispersal pattern for the founding individuals of the first two long-term wolf territories in each state (Figure 3b), because, for these individuals the natal territories were available from the German wolf database (DBBW, 2017).

For each territory that has been established between 2000 and 2015, we analyzed two key habitat variables that determine habitat suitability for wolves in neighboring Poland – forest cover and road density (Jedrzejewski et al., 2008). The habitat values were extracted from CORINE Land Cover classification raster data (2012) and the Digital Landscape model of the German Federal Agency for Cartography and Geodesy (Bundesamt für Kartographie und Geodäsie, 2018).

Finally, we analyzed wolf mortalities from 2000 to 2015 using the publicly available German wolf database (DBBW, 2017) where the cause of each mortality event is classified as anthropogenic (traffic or poaching), natural, or unknown. We included only mortality events found within known wolf territories (n = 92) and assigned each mortality location to MTA or PA within a 1 km buffer or to other area. For each of the three location types, we calculated the number of "territory years," that is the cumulative number of years territories of each location type existed. This allowed us to score the amount of mortality cases found in each location type relative to the number of wolf territories and the time they had been occupied. We used Pearson's chi-squared test with simulated P-values (based on 2000 replicates) for comparing the number of mortalities relative to "territory years" among MTAs, PAs, and other areas.

3 | RESULTS

We found that the increase of wolf reproductive units in Germany from one unit in 2000 to 67 in 2015 followed an exponential growth curve with a 36% increase per year (Figure 1a).

The first three wolf territories were located on an active MTA in Saxony. The three subsequent territories were established in their immediate surroundings forming together a relatively small initial colonization area (Figure 1b and Supplemental Figure 1). In 2007, the first two wolf territories outside the initial colonization area were established more than 200 km away on two MTAs (Supplemental Figure 1). In the following years, more territories were established in new federal states, long distances from the nearest reproducing pack.

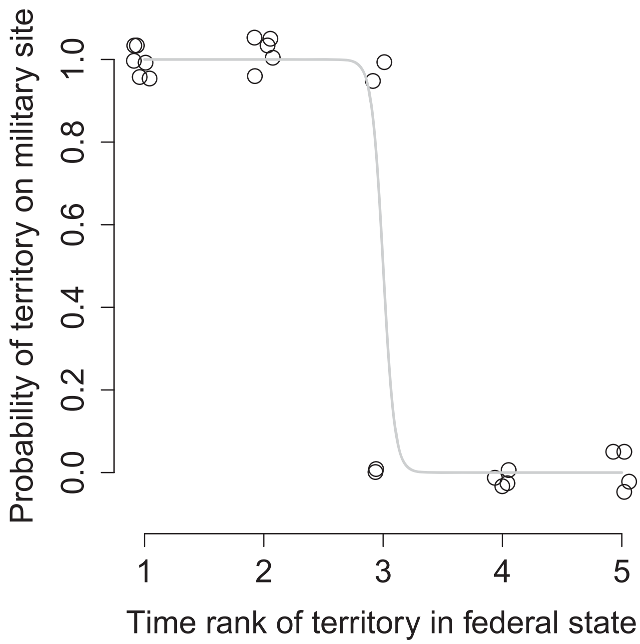

FIGURE 2 Probability of territory establishment on MTAs relative to their order of establishment (time rank) in each state (n = 23 territories from six states). The gray curve represents a logistic model fit. Note that no territories on protected areas were among the first three in any state (not shown)

We found the first and second long-term territory in each of these newly colonized states were always established on active MTAs (Figure 2 and 3a and 3b). None of the initial territories were established on PAs or other areas.

Between 2000 and 2015, 16 out of 79 territory establishments took place on active MTAs, 9 on PAs, and 54 in other areas. For wolves founding a new territory on a MTA, the average minimum dispersal distance was considerably greater (128 km, median 165 km) than for wolves that established their territories on PAs (64 km, median 31 km, $\beta = -0.356.27$, $P < 0.05$) or on other areas (38 km, median 20 km, $\beta = -0.596$, $P < 0.001$; Figure 4).

Some of these initial recolonizing events in new federal states far away from the next source pack served as stepping-stones allowing subsequent colonization in the surroundings areas (Figure 1 and Supplemental Figure 1). In 2015, 13 out of 21 MTAs (62%) with a minimum size of 30 km^2 were occupied by wolves, but only 8 out of the 55 (14%) PAs of the same size class were occupied.

We found no significant difference between MTA territories and PA territories in the two key habitat variables forest cover (mean MTA: 52%, mean PA: 50%, t value = –0.263, $P > 0.1$) and road density (mean MTA: 0.48 km km^{-2}, mean PA: 0.59 km km^{-2}, t value = 0.601, $P > 0.1$; Supplemental Figure 2). Likewise, the amount of forest cover was not different between MTA territories and other territories (mean other areas: 47%, t value = –1.001, $P > 0.1$). The only significant habitat difference we found was in the road density

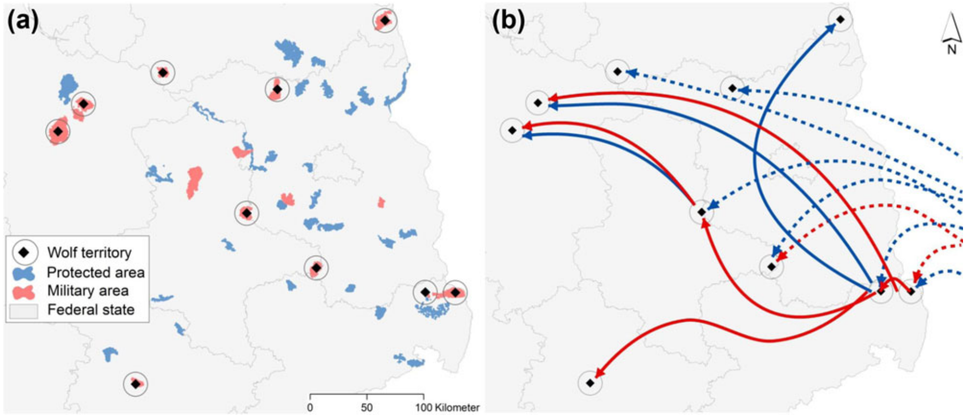

FIGURE 3 Establishment patterns of the first two permanent territories per federal state from 2000 until 2015. (a) The first territories were always established on MTAs. (b) Origin of the founder animals of the first long-term territories. Red arrows: females, blue arrows: males. Dotted lines: individual immigrated from Poland. Solid lines: Individual dispersed from known pack in Germany (for Brandenburg only territories outside the initial colonization area were considered in Figures 3a and 3b)

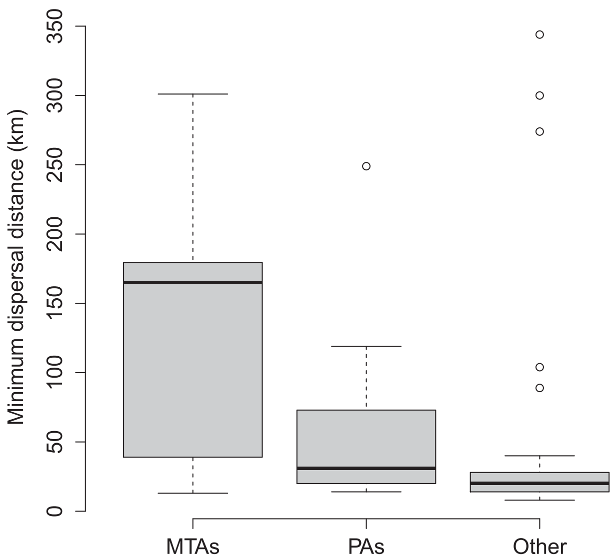

FIGURE 4 Median and range of minimum dispersal distances for wolves establishing territories on MTAs, PAs, and other areas

between MTA territories and other territories (mean other areas 0.61 km km^{-2}, t value = 2.385, $P < 0.05$).

Anthropogenic mortality was the prevailing mortality cause accounting for 80% ($n = 74$) of recorded deaths within territories. Anthropogenic fatalities were lower on MTAs compared to other areas (relative to the total territory years in these location types [see Table 1], chi-square = 9.65, $P < 0.01$). There was no difference between anthropogenic fatalities on PAs compared to other areas (relative to the total territory years in these location types [see Table 1], chi-square = 0.59, $P = 0.46$). Mortality due to poaching was higher on PAs than on MTAs, although the sample size was relatively low (Table 1; chi-square = 13.41, $P < 0.001$).

4 | DISCUSSION

This is the first study that examines the role of active MTAs in facilitating the recolonization of a previously extirpated large carnivore in a highly human modified landscape. The rapid rate of population increase and range expansion of wolves in Germany was facilitated by the presence of MTAs. These sites, rather than PAs, acted as stepping-stones promoting the recolonization of new areas far away from the next source pack.

This form of jump expansion with initially large gaps between wolf territories was previously reported from other regions (Nowak & Mysłajek 2016; Wabakken, Sand, Liberg, & Bjärvall, 2001; Wydeven, Schultz, & Thiel, 1995). Unique about the expansion in Germany is that MTAs were exclusively used as stepping-stones. Once wolves established territories and bred on MTAs a subsequent diffusion like range expansion around these initial colonization areas could also be observed. There are three potential explanations for the initial preference of active MTAs: (1) habitat preference, (2) natal habitat preference, or (3) mortality risk.

1. MTAs are known to play an important role for conservation as they harbor disproportionally high numbers of threatened and endangered species (Stein, Scott, & Benton, 2008; Warren et al., 2007). Biodiversity on these sites is often high even compared to national parks (Arimoro et al., 2017; Aycrigg et al., 2015; Flather, Joyce, & Bloomgarden, 1994; Groves et al., 2000; Stein et al., 2008; Warren et al., 2007). The conservation effect of MTAs is often linked to an artificially maintained patchiness favoring species richness in plants (Jentsch, Friedrich, Steinlein, Beyschlag, & Nezadal, 2009; Molino & Sabatier 2001), invertebrates (Cizek et al., 2013; Warren & Büttner, 2008), and birds (Gazenbeek, 2005). In

TABLE 1 Number of territory years (cumulative number of years territories were occupied) and the number of wolves found dead within territories

Location	Territory years	Mortality total	Mortality traffic	Mortality poaching
Military training areas	103	17 (0.16)	13 (0.13)	0 (0.0)
Protected areas	42	15 (0.36)	5 (0.12)	6 (0.14)
Other areas	142	60 (0.42)	44 (0.31)	6 (0.04)

Locations where carcasses were found were classified per location type as military training area, protected area, or other area. Traffic and poaching mortality sums up to anthropogenic mortality. Total mortality includes anthropogenic, natural, and unknown (the latter two not shown). The number in brackets denotes mortality cases found per territory year.

providing and maintaining rare habitat conditions, MTAs may serve as refugee areas especially for some habitat specialists (Jentsch et al., 2009; Warren & Büttner, 2008). Wolves, however, are habitat generalists that are known to adapt to a wide variety of ecological conditions (Fritts, Stephenson, Hayes, & Boitani, 2003). Among Europe's large carnivore species, wolves are the most successful in adapting to human-dominated landscapes (Chapron et al., 2014). This habitat adaptability of wolves is also evident in Germany where after the initial establishment of territories on MTAs subsequent territories were established in other areas. In addition, we did not find significant differences in key habitat variables between MTA territories and PA territories. Forest cover did not differ between MTA territories and PA territories nor did road density. If forests would have played a key role in the colonization process, we would have expected the large forest complexes of north-east Germany close to the Polish border and source population (Czarnomska, Borowik, Niedziałkowska, Stronen, & Nowak, 2013) to be recolonized first (Reinhardt & Kluth, 2007; BMUB, 2015). However, wolves did not settle there until 2015 (Supplemental Figure 1). Differences in habitat type or road densities thus cannot explain the preference of MTAs. Because densities of wild ungulates, the main prey of wolves in Germany (Wagner, Holzapfel, Kluth, Reinhardt, & Ansorge, 2012), are high in all areas settled by wolves to date (Reinhardt & Kluth, 2007), it is also implausible that different prey densities could serve as an explanation. Overall, it is unlikely that habitat suitability alone was the primary driver for the strong initial selection for MTAs by wolves.

2. The preference for MTAs may be partly explained with natal habitat preference. Natal habitat preference has been shown in a variety of species where dispersing animals tend to choose habitat types similar to those where they have been raised (overview in Stamps & Davis, 2006). Indeed, seven out of eight wolves with known natal territories (i.e., wolves born in Germany) that settled on MTAs have also been raised on MTAs (Figure 3b). For the wolves emigrating from Poland, the natal territories remain unknown. We believe it is unlikely that most of these wolves were raised on MTAs, because MTAs did not play a critical role during wolf recolonization in Western Poland (Nowak & Mysłajek 2016; Nowak et al., 2017). While it is possible that natal habitat preferences play at least some role in the colonization process, additional research would be needed for conclusive evidence.
3. The initial preference for active MTAs may at least partly be linked to the lower level of anthropogenic mortality on MTAs compared to other areas, including PAs. PAs did not show a lower mortality rate when compared to other areas. Traffic incidents are relatively low on MTAs because of the low frequency of public roads, but this is also true for PAs. The second component of anthropogenic mortality is poaching. Poaching potentially plays a greater role than we estimate here because most poaching events remain undetected (cryptic poaching) (Liberg et al., 2011). One key difference between MTAs and other areas, including PAs, is the hunting regime. In Germany, hunting on MTAs is supervised by federal authorities and is managed across large areas, whereas PAs and other areas usually are divided in private hunting grounds with a minimum size as small as 75–150 ha. This may lead to situations where a wolf pack shares its territory with more than 100 hunters which, in turn, make these territories more vulnerable to poaching even if most hunters do not poach. For many PAs, the hunting regime often follows the same small-scale approach because landownership is often fragmented, including private lands (with the exception of national parks). Therefore, opinions and attitudes of land owners and hunters on protected and other areas may differ considerably leaving more opportunity for illegal killings than on strictly and uniformly managed MTAs. This may explain why we found lower poaching rates on MTAs versus PAs. We believe it unlikely that our findings on low mortality on MTAs are a result of lower detectability of carcasses in these areas. Although these sites are closed for the public, they are intensely used by armed forces and forestry and subject to a wide range of environmental monitoring programs.

Overall, for the rapid recolonization of wolves in Germany MTAs uniquely served as stepping-stones despite wolves settling on MTAs had to disperse longer distances during the early years of population recovery as compared to wolves that settled near their natal territories. A contributing factor seems to have been the lower mortality rate on MTAs. At very low population densities, anthropogenic mortality may have had an additive effect on the wolf population and may have been simply too high outside MTAs ultimately shaping this unique colonization pattern. A similar additive effect of anthropogenic mortality at low population density has been shown for the red wolf (*C. rufus*) (Sparkman, Waits, & Murray, 2011). At today's population densities however, the anthropogenic mortality rate seems to be less critical and rather compensatory allowing for a robust population growth.

4.1 | Management implications

MTAs are known to be important conservation areas (Lindenmayer et al., 2016; Zentelis et al., 2017), but their beneficial effect on large mammalian species at larger scales has received little attention to date. The beneficial effect may extend well beyond the wolf example of this study (Arimoro et al., 2017; Zentelis & Lindenmayer 2015). Though MTAs are under the influence of human activity and disturbance, they tend to be less fragmented than other areas (Ibisch et al., 2016) and serve as refugia in highly human-dominated landscapes. MTAs in Germany are the largest land use category with a unified management of the federal government. The hunting regime on MTAs is homogeneous over a large area and may provide less opportunity for poaching.

We conclude that MTAs especially in highly fragmented Europe are key areas for large carnivore conservation and make a substantial contribution to conservation outside the formal protected area network (Lindenmayer et al., 2016). When these areas are taken out of military use, particular attention should be paid on how to maintain their function as refugia for species conservation (Cizek et al., 2013). The listing of large parts of current and former MTAs as Natura 2000 areas is a first step to preserve their conservation function. However, we recommend the strict hunting management for MTAs should continue after the sites become inactive.

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AUTHOR CONTRIBUTIONS

IR and TM conceptualized the paper, IR analyzed the data, and all authors contributed to the writing of the manuscript.

CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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SUPPORTING INFORMATION

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

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