Review on Agriculture and Rural Development 2022 vol. 11 (1-2) ISSN 2677-0792
DOI: 10.14232/rard.2022.1-2.46-53

THE REASONS FOR THE RANGE EXPANSION OF THE GREY WOLF, COYOTE AND RED FOX

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ABSTRACT
Canidae is a species-rich, abundant, and widespread family. Several wild canid species, in particular, have shown a significant range expansion and increased abundance in the last few decades or even in the last century. The grey wolf (*Canis lupus*), coyote (*Canis latrans*), and the red fox (*Vulpes vulpes*) are resident on whole continents or even on multiple continents. Although canids share common behavioural and ecological characteristics, the combination of species-specific elements contributes to their success. This review investigated which factors have contributed mainly to the expansion of the grey wolf, coyote, and red fox. Analysis of the literature review shows that the grey wolf has benefitted from legal protection, reintroduction programs, and the ability to colonise areas naturally because of its particular social system, early reproduction, high fecundity, and rapid physical development. As a meso-carnivore, the coyote has shown a rapid spread after the extermination of apex predators in several regions in North America. Along with changes in land use, their high adaptability and hybridisation with wolves have all contributed to their prolonged success. The red fox has shown the largest expansion among canids even though it is a solitary species. Their morphological, reproductive and behavioural traits have facilitated their expansion to all corners of the world. Moreover, the species benefitted from human-caused changes like land conversion and the almost complete eradication of rabies in Europe. Overall, it is crucial to change management policies for grey wolves and increase control measures to regulate the three species and mitigate (potential) human-carnivore conflicts.

Keywords: wild canids, human-carnivore conflict, expansion, population increase

INTRODUCTION

The Canidae family is the most widely distributed family of eutherian predators and is highly diverse (MACDONALD ET AL., 2019). Among them, the grey wolf (*Canis lupus*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*) have shown one of the highest successes in terms of colonisation (red fox and coyote) and recolonisation (grey wolf) in the last few decades and century. Moreover, these species are seen as a trophic cascade, where top-down processes (direct and indirect effects of interspecific competitive killing) can influence the spatial distribution of the species (NEWSOME & RIPPLE, 2015) as the grey wolf, golden jackal (*Canis aureus*), and red fox are part of the carnivore guild. Generally speaking, the ecology of a species highly influences its dispersal behaviour, this in combination with environmental changes can cause shifts in their distribution. Consequently, such range expansions can cause new challenges and confusion for management and policy, especially if they contribute to new conflicts (TROUWBORST ET AL., 2015). These conflicts include predation on livestock, game species, endangered wildlife, and sometimes even attacks on humans or pets (TREVES & NAUGHTON-TREVES, 1999; SILLERO-ZUBIRI & LAURENSON, 2001). The fact that these expansions are present across several parts of the world raises questions on what allowed these various canid species to achieve such wide distributions, high abundances, rapid expansion, (re)colonization and biological invasion, and resilience to human population control in their given range (MACDONALD ET AL., 2019). Thus, similar to the diagnosis of population declines (CAUGHLEY & GUNN, 1996), it is crucial to understand these underlying mechanisms in order to effectively manage these species and reduce human-carnivore

conflicts. This paper studies the traits of the wolf-coyote-fox triplet of the carnivore guild. Indeed, in the European context, regarding ecological roles and interactions, the coyote can be replaced with the golden jackal as speculated by some authors (POTTS, 2012). However, as the documentation of the golden jackal's expansion and its underlying reasons is still in its early stages, therefore, this study can be a baseline for the wolf-jackal-fox triplet.

MATERIALS AND METHODS

A general literature review was conducted on the range expansion of the grey wolf, coyote, and red fox and the reasons for it by using Google Scholar as the main search engine. The search terms used were the species ("grey wolf", "coyote", "red fox") followed by "range" AND "expansion" AND "reasons" OR "causes" OR "population increase", e.g., "coyote range expansion causes". However, "reasons" and "causes" were left out if no appropriate papers were found, as studies that cover the range expansion of the species often include the reasons for it as well. Papers from all years were used. Due to the high number of results, only papers were selected that covered the topic of this review. When an appropriate paper was found, also the publications therein were analysed. The number of papers used was 19 for the grey wolf; 16 for the coyote; and 11 for the red fox. The list of scientific documents is not exhaustive and does not include all studies related to this topic. However, the list of publications is sufficient to provide a comprehensive overview of the current distribution of the three species and an explanation as to why they are exceptionally successful in their range expansion.

RESULTS

The grey wolf

The grey wolf is one of the most extensively studied canids (VUCETICH ET AL., 2011) and is considered an apex predator (RIPPLE ET AL., 2014a) with only top-down and often regulatory impacts (PETERSON ET AL., 2014). They are considered the most important predator (apart from humans) of cervids in the Northern Hemisphere, due to their wide geographic distribution, method of hunting, and year-round activity (PETERSON *ET AL*, 2003). Wolves were driven to the brink of extinction in the 1800s in North America and Europe and are now returning to their formal range (PHILIPS ET AL., 2004). In the past, the wolf used to be the most widely distributed canid throughout Europe, Asia, and North America and they occupied a variety of habitats, including deserts, Mediterranean shrubland, coniferous forests, and frozen tundra (MECH, 1970). However, in the last few centuries, they have decreased in numbers due to persecution and habitat fragmentation, resulting in a global reduction in their historical range to 68% (YOUNG & GOLDMAN, 1944; HUNTER, 2011; RIPPLE ET AL., 2014b). In the last few decades, however, the wolf population has started to increase because of enhanced legal protection, reintroduction programs, and natural recolonisation, which resulted in recovered populations in both North America and Europe (RIPPLE ET AL., 2014b). In Europe, the recolonisation started at the beginning of the 2000s, moreover, the wolf is immigrating Central Europe from the Carpathians, Balkans, and Baltic populations (DE GROOT ET AL., 2016; HERZOG, 2018; SZEWCZYK ET AL., 2019). One of the most viable wolf population in Europe can be found in the Baltic region, which consists of approximately 3600 individuals and inhabit territories of Estonia, Latvia, Lithuania, Belarus, northeastern Poland, northern Ukraine, and the western part of the Russian Federation (LINNELL ET AL., 2008; OZOLIŅŠ ET AL., 2011). In Latvia, the wolf has never been totally exterminated unlike in other parts of Europe (ŠUBA ET AL., 2021). Moreover, natural recolonisation was probably enhanced by

the high mobility of the grey wolf which allows them to rapidly disperse over distances up to 900 km, which has been one of the longest documented dispersals for a terrestrial mammal (FRITTS, 1983). Dispersing individuals were reported to cross four-lane highways and avoid lakes and cities (MERRILL & MECH, 2000). Additionally, the grey wolf has a social system (packs) that allows for cooperation, which aids in hunting, food defence, and higher reproductive success (MACDONALD ET AL., 2019). Wolves have an early first reproduction (two years old), high fecundity (five to six pups per litter), and rapid development (80% of the full body size is achieved by the end of the first year) (FULLER ET AL., 2003). These traits make grey wolves, but also other similar canids, more adaptive to new environments. Thus, facilitating their rapid expansion.

The coyote

The distribution of the coyote has rapidly expanded in North and Central America since 1900 during a period when most other mammals were declining (HODY & KAYS, 2018). Their expansion started around 1900 when they moved north into taiga forests, east into deciduous forests, west into coastal temperate rainforests, and south into tropical rainforests (HODY & KAYS, 2018). The expansion of the coyote shows to be still in motion towards eastern Canada and in Mexico. Coyotes have expanded their geographic range by approximately 40% since the 1950s, which is at least twice as much as any other carnivore during that period in North America (LALIBERTE & RIPPLE, 2004). Prior to European settlements, the coyotes were restricted to prairie ecosystems between the Mississippi River and the Rocky Mountains from southern Canada to central Mexico (PARKER, 1995). Coyotes then expanded towards the west in the late 1800s, followed by multiple expansions during the 1900s (PARKER, 1995). There are several reasons that could explain the rapid expansion of the coyote. Similar to the golden jackal (KROFEL ET AL., 2017; NEWSOME ET AL., 2017), the extirpation of apex predators probably facilitated the expansion process by reducing predation risk and allowing coyotes to expand their niche to larger prey (HODY & KAYS, 2018). Mainly the disappearance of wolves and cougars across most of the eastern part of North America and the decline of cougars and jaguars in Central America aided in the colonisation of the coyote (BEKOFF & GESE, 2003; BERGER & GESE, 2007). Another factor for expansion is land conversion; forested areas that were changed into agricultural landscapes in eastern North America and Central America likely provided a suitable habitat that was not suited previously (PARKER, 1995). These opened additional landscapes provided habitat not only for the coyotes but also for prey species such as the white-tailed deer (GOMPPER, 2002). However, deforestation did not happen everywhere on the continent. In western Canada and Alaska, the creation of human settlements might have facilitated the expansion during the gold rushes in the late 1880s (MOORE & PARKER, 1992). However, this explanation has not been critically studied (HODY & KAYS, 2018). Moreover, coyotes are one of the few carnivore species that occur in urban areas and have been described as behaviourally misanthropic and demographically synanthropic (GEHRT ET AL., 2011; GRINDER & KRAUSMAN, 2001; BRECK ET AL., 2019). Although they show strong spatial and temporal avoidance of humans, they have high survival, density and reproduction in urban areas (GEHRT ET AL., 2011). Overall, the coyote is an opportunistic species with a high adaptation capability (FLEMING ET AL., 2017), which aids the species in their rapid dispersal and ability to thrive in human-dominated landscapes. Additionally, it is speculated that hybridization with eastern wolves (*Canis lycaon*) (and domestic dogs) could have facilitated the expansion as well (HODY & KAYS, 2018), by introducing new genotypes that conferred a selective advantage that provide high adaptive potential into habitats in eastern North America, which could increase overall fitness (WAY, 2013; THORNTON & MURRAY, 2014; WAY & LYNN, 2016).

The red fox

The red fox is the world's most widespread canid species (other than the domestic dog) and an archetypal generalist mesopredator (FLEMING ET AL., 2017). The red fox lives predominantly solitary and is the most common sympatric competitor with the golden jackal (SCHEININ ET AL., 2006). Currently, it is distributed throughout Europe, North America, Asia and Australia, and its wide range can be attributed to its morphological, reproductive and behavioural traits that can facilitate efficient temperature regulation, an extremely broad dietary range and a high tolerance for persecution (LARIVIÈRE & PASITSCHNIAK-ARTS, 1996). Because of their opportunistic scavenging behaviour, red foxes can easily adapt to anthropogenic food sources like refuse, garden produce, poultry, and small rodents (FLEMING ET AL., 2017). Both urban and rural, and also peri-urban environments have high numbers of foxes (BINO *ET AL*., 2010). Therefore, foxes can benefit from the conversion of homogeneous vegetation into fragmented, heterogeneous landscapes that provide larger foraging diversity and shelter opportunities (WHITE ET AL., 2006). Moreover, due to land conversion, densities or activity of higher-order predators could be reduced through persecution or reducing habitat quality, which in turn could benefit red foxes (FLEMING ET AL., 2017). According to PASANEN-MORTENSEN ET AL.,. (2013), red fox populations in Eurasia were limited by Eurasian lynx. Additionally, in North America, coyotes can limit red fox densities (HARRISON *ET AL*., 1989), while red fox populations benefit from the suppression of coyotes by grey wolves (NEWSOME & RIPPLE, 2015). Moreover, a large part of the species distribution is because of human-assisted dispersal for either fur harvesting or recreational hunting (SAUNDERS ET AL., 2010). Another reason for its expansion is the vaccination against rabies (CHAUTAN ET AL., 2000). The oral vaccination program in Europe started as early as 1978 (STÖHR & MESLIN, 1996) and since then, the rex fox has been able to recover and increase in the long-term in many European countries (CHAUTAN ET AL., 2000).

DISCUSSION

The grey wolf, coyote, and red fox are one of the most successful wild canids and have shown a large expansion in their range (*Table 1*). Thanks to their generalist nature, adaptability, flexibility, high mobility and capacity for long-distance travel, high reproductive rate, and sociability and ability to cooperate (MACDONALD ET AL., 2019), they are able to quickly colonise new areas.

Table 1 Summary of the reasons for range expansions for the grey wolf, coyote, and red fox

	Reasons for range expansion
Grey wolf	Legal protection; reintroductions by humans; high mobility, strong social system (packs), early first reproduction, high fecundity, and rapid development
Coyote	Extirpation of apex predators; land conversion; opportunistic and highly adaptable which allows for high survival and reproduction in urban areas; hybridisation with wolves ("coywolf")
Red fox	Opportunistic, morphological, reproductive and behavioural traits that facilitate efficient temperature regulation, which allows for a broad dietary range and a high tolerance for persecution; benefit from fragmented, heterogeneous landscapes; human introduction for fur harvesting or recreational hunting; vaccination against rabies

However, to effectively manage or conserve a species, it is necessary to look at the individual species' ecology itself (CAUGHLEY & GUNN, 1996). Moreover, not only the ecology of the species contributes to its range expansion but due to global environmental changes, species are shifting their distributions, although these factors are difficult to influence. Therefore, it is necessary to look at policies and regulations as well. For example, out of the three canids, the grey wolf is protected in many European countries with no active interventions (HERZOG, 2018) and causes many human-wolf conflicts (FERNÁNDEZ-GIL ET AL., 2016; AMBRALI, 2019; KUIJPER ET AL., 2019). Overall, in an ideal situation, a local differentiation and a combination of different management methods should be applied; i.e., local killings of problematic individuals, sustainable utilisation, prevention of diseases (e.g., rabies), herd protection measures, and a management concept that has been developed from a participatory process, all depending on the stage of expansion of the specific species (HERZOG, 2018). However, as KUIJPER ET AL., (2019) point out, the solutions are too focused on reactive approaches and do not focus on the root cause or proactive management. Thus, mitigating human-carnivore conflicts should include strengthening the separation between humans and wild canids (KUIJPER ET AL., 2019) along with tangible, practical approaches.

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